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Editor:

N. RASHEVSKY

Associate Editors:

H. D. LANDAHL; ANATOL RAPOPORT

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BULLETIN OF
MATHEMATICAL BIOPHYSICS
VOLUME 13, 1951

ON DOMINANCE RELATIONS AND THE STRUCTURE OF ANIMAL SOCIETIES: I. EFFECT OF INHERENT CHARACTERISTICS

H. G. LANDAU
COMMITTEE ON MATHEMATICAL BIOLOGY
THE UNIVERSITY OF CHICAGO

Societies are considered in which a non-transitive dominance relation exists between every pair of members, such as the peck-right in a flock of hens. A one-dimensional measure of the structure of such a society, h, is defined, with $h = 0$ for equality and $h = 1$ for the hierarchy. It is assumed that each member of the society is characterized by an ability vector whose components depend on individual characteristics such as size, concentration of sex hormone, etc., but not on social factors such as social rank. The distribution of abilities among members of the society is assumed to be given by a distribution function which is the same for all members, and the probability that one member dominates another is given by a function of the ability vectors of the two.

On these assumptions formulas for the expected (mean) value and variance of h are determined in terms of the distribution and dominance probability functions. Some special cases are calculated, especially that for normally distributed abilities and dominance probability given by the normal probability integral.

Several conclusions are derived. If all members are of equal ability, so that dominance probability is 1/2, then any sizable society is much more likely to be near the equality than the hierarchy; and, as the size of the society increases, the probability that it will be near the hierarchy becomes vanishingly small. If the dominance probability is a weighted sum of several independent components, which make up the ability vector, then the society is less likely to be close to the hierarchy as the number of these components increases. The hierarchy is the prevalent structure only if unreasonably small differences in ability are decisive for dominance. From this it appears that the social factors, or psychological factors such as the previous history of dominance, which are not included in the present treatment, may be of great importance in explaining the observed prevalence of structures very close to the hierarchy in flocks of domestic hens.

1. INTRODUCTION. It was observed by T. Schjelderup-Ebbe (1922) that between every two hens in a flock there exists a relation known as the "peck right" which establishes the dominance of one hen over the other. Similar dominance relations have been observed in social groups of many other vertebrates, although not always as clearly defined as in domestic hens and not always holding between every pair of members of the group. These relations have been intensively studied by W. C. Allee (1938, 1949) and his students

(Potter, 1949; Collias, 1943; Guhl and Allee, 1944) using mainly domestic hens.

The mathematical theory of such dominance relations has been investigated by A. Rapoport (1949a, 1949b, 1950), and in the following we make use of some of the concepts introduced by him. Some suggestions toward a theory were also given by C. C. Lienau (1947).

We shall be concerned with societies containing a finite number, n, of members with a dominance relation holding between the two members of every pair. A dominance relation is a binary, asymmetric, non-transitive relation, j dominates k being written $j > k$.

Although the motivation and most of the applications of this study are from animal societies it should be remarked that there are other examples of dominance relations. Any tournament—chess, tennis, etc.—consisting of a single round robin with no games ending in draws is an example. If the tournament is a multiple round robin (each contestant plays more than one game with every other one), the member of each pair who wins the majority of the games between them can be said to dominate the other. The baseball leagues are examples. Dominance relations also occur in the von Neumann-Morgenstern theory of games (von Neumann and Morgenstern, 1947) where they are needed to define a solution. These writers also point out that the same idea, i.e., a pairwise ordering without transitivity, occurs in the "paper-form" in sports and races, comparisons of the strength of chess players in a tournament, etc.

A complete description of the structure of a society with a dominance relation requires, of course, the statement of the $n(n-1)/2 = \binom{n}{2}$ dominance relations between all the pairs of members of the society. This statement is most conveniently formulated as a matrix (a_{jk}) where

$$\begin{aligned} a_{jk} &= +1 \quad \text{if } j > k, \\ a_{jk} &= -1 \quad \text{if } k > j, \\ a_{jj} &= 0, \quad j = 1, 2, \cdots, n \end{aligned}$$

(Lienau, 1947). However, this matrix is not unique because renaming the members, that is, permuting rows and corresponding columns of the matrix, does not change the structure of the society. Thus the structure is given by the set of matrices which can be obtained from a given one by any permutation of rows and the same permutation of columns.

A geometric (topological) description of the structure can also be given by n points with lines connecting every pair of these points and a direction assigned to every line.

Let us call the structure, when thus completely defined, the "dominance structure" to distinguish it from another definition of structure introduced below. It is easily possible to find a lower bound for the number of possible dominance structures. There are $2^{\binom{n}{2}}$ different matrices which can be obtained by assigning either $+1$ or -1 to the $\binom{n}{2}$ elements a_{jk} which are above the principal diagonal, $j < k$; the a_{jk} below the principal diagonal are then determined. When the $n!$ permutations of n objects are applied to the rows and columns of any one matrix it will go into at most $n!-1$ of the other matrices. Hence there must be at least $2^{\binom{n}{2}}/n!$ different dominance structures. This number becomes very large even for moderate n. For $n = 8$ there are over 6,000 possible dominance structures, and for $n = 12$ there are more than 10^{11}.

2. SCORE STRUCTURE AND HIERARCHY INDEX. Our aim is to characterize the structure of the society under certain assumptions about the properties of the members. For this purpose we do not use the dominance structure, but a simpler definition of structure, the score structure, and from it derive a one-dimensional measure of the structure, the hierarchy index, with which we shall be mainly concerned.

The score structure, V, of a society is a set of n integers $V = (v_1, v_2, \cdots, v_n)$, where v_j means that the jth member dominates v_j of the others. Any permutation of the v_j does not, of course, alter the score structure. This definition of structure was introduced by Rapoport (1949a) but without the name used here.

The score structure can be obtained from a dominance structure matrix by adding the +1's in each row. A little consideration shows that more than one dominance structure can give the same score structure. The simplest example occurs for $n = 5$. The following two matrices

$$\begin{bmatrix} 0 & 1 & 1 & 1 & -1 \\ -1 & 0 & -1 & 1 & 1 \\ -1 & 1 & 0 & -1 & 1 \\ -1 & -1 & 1 & 0 & 1 \\ 1 & -1 & -1 & -1 & 0 \end{bmatrix} \quad \text{and} \quad \begin{bmatrix} 0 & 1 & 1 & -1 & 1 \\ -1 & 0 & 1 & 1 & -1 \\ -1 & -1 & 0 & 1 & 1 \\ 1 & -1 & -1 & 0 & 1 \\ -1 & 1 & -1 & -1 & 0 \end{bmatrix}$$

both have $V = (3, 2, 2, 2, 1)$, but they cannot be equivalent under row and column permutation because in the first matrix $5 > 1$ with $v_5 = 1$ and 1 dominates all the others, whereas in the second $4 > 1$

with $v_4 = 2$, and again 1 dominates all the others. Thus V is a less complete definition of the structure derived from the dominance structure. It will not suffice for all purposes, as will be discussed in a later paper, but can be used for our present purpose which is to show the conditions under which the structure approaches the hierarchy.

The hierarchy is the structure with $V = (n-1, n-2, \cdots, 0)$ so that the members of the society can be ordered

$$1 > 2 > 3 > \cdots > n$$

with each dominating all the members below it and being dominated by all those above. At the opposite extreme is what we call the "equality" with

$$v_1 = v_2 = \cdots = v_n = \frac{n-1}{2}, \tag{1}$$

which can occur exactly only for n odd.

As a one-dimensional measure of the position of any society with respect to the extremes of equality and hierarchy we introduce the "hierarchy index,"

$$h = \frac{12}{n^3 - n} \sum_{j=1}^{n} \left(v_j - \frac{n-1}{2} \right)^2 . \tag{2}$$

The hierarchy index has the range 0 to 1, the factor $12/(n^3 - n)$ being chosen to make $h = 1$ when V is the hierarchy and, of course, $h = 0$ for equality. The quantity, h, is simply a multiple of the variance of the v_j since $(n-1)/2$ is the mean of the v_j.

The remainder of this paper is concerned with the investigation of h. We shall find that it gives a great deal of information about how the structure of the society depends on the properties of its members. Lienau (1947) thought that it would not be possible to define a useful one-dimensional measure of structure, but we hope to show that h does fulfill this function.

3. PROPERTIES DETERMINING DOMINANCE.

The actual structure of the society will depend on what assumptions are made about the properties of the members. The model used here is a generalization of that introduced by Rapoport (1950) and would appear to be sufficiently broad to include most of the factors making for dominance in animal societies, except social factors. Some excluded factors which limit its applicability are pointed out below.

It is assumed that each member is characterized by an "ability vector," $x_j = (x_{j1}, x_{j2}, \cdots, x_{jm})$. These x_{ja} measure the individual characteristics which make for dominance such as size, concentration of male sex hormone, etc. (Collias, 1943). However, they do not depend on the social characteristics such as v_j.

We now introduce probability concepts. For the definitions and statements of the methods and theorems used we refer to H. Cramér (1946). It is assumed that the abilities are distributed among the members of the society according to the multivariate distribution function $F(x) = F(x_j)$, $j = 1, 2, \cdots, n$. Assuming that the distribution is the same for all members of the society means assuming that it is homogeneous, all members being of the same breed. The modification needed to take into account societies of mixed breeds, as were used in the experiments of J. H. Potter (1949), would not be difficult, although the statement of the results would be more complicated.

For given values of x_j and x_k it is assumed that the probability that j dominates k is given by a function of the two vectors $p(x_j, x_k) = p_{jk}$, i.e.,

$$Pr\,[j > k] = p(x_j, x_k) = p_{jk}, \quad j, k = 1, 2, \cdots, n. \tag{3}$$

Since p_{jk} is a probability we must, of course, have

$$0 \leq p_{jk} \leq 1, \tag{4}$$

and since either $j > k$ or $k > j$, we have

$$p_{jk} + p_{kj} = 1. \tag{5}$$

We do not attempt to discuss here the problem, or even the possibility, of determining the functions $F(x)$ and p_{jk} from observations on societies. The latter is the identification problem which is discussed by T. C. Koopmans and O. Reiersøl (1950). It appears from the results below that under certain assumptions on the form of $F(x)$ and p_{jk}, these functions may not be completely identifiable on the basis of observations on the structure of societies, that is, not completely determined from such observations. However, the indeterminism appears to be of not a very essential nature; and more important, planned experiments like the paired combats carried out by Collias (1943) should permit direct determination of these functions.

4. EXPECTED VALUE OF h.

We denote the mean, or expected, value of a random variable, y, by $E(y)$. Now

$$E(h) = \frac{12}{n^3 - n} \sum_{j=1}^{n} E\,[(v_j - \bar{v})^2]\,, \tag{6}$$

where $\bar{v} = (n-1)/2$ is the mean of each v_j. Since $F(x_j)$ is the same for all j, and p_{jk} is the same function of x_j and x_k for all j and k, the n terms in the summation in (6) will be the same, so that

$$E(h) = \frac{12}{n^2 - 1} E\,[(v_1 - \bar{v})^2]\,. \tag{7}$$

If $x_1, x_2, \cdots, x_n$ are fixed, then the probability that $v_1 = v$ is given by

$$Pr\,[v_1 = v] = \sum p_{1j_1} p_{1j_2} \cdots p_{1j_v} p_{j_{v+1}1} p_{j_{v+2}1} \cdots p_{j_n 1}\,, \tag{8}$$

where j_1 to j_v are any v of the $n-1$ integers $2, \cdots, n$ and j_{v+1} to j_n are the remaining $n - 1 - v$, and the summation is over all terms of this type. This is the same as the sum of the terms in the expansion of

$$\prod_{j=2}^{n} (p_{1j} + p_{j1}) \tag{9}$$

which contain v factors p_{1j} and $n - 1 - v$ factors p_{j1}. The characteristic function of v_1, i.e., $E(e^{itv_1})$ is then

$$E(e^{itv_1}) = \prod_{j=2}^{n} (p_{1j} e^{it} + p_{j1})\,, \tag{10}$$

the characteristic function of $v_1 - \bar{v}$ is

$$\begin{aligned} E(e^{it(v_1 - \bar{v})}) &= e^{-it\left(\frac{n-1}{2}\right)} \prod_{j=2}^{n} (p_{1j} e^{it} + p_{j1}) \\ &= \prod_{j=2}^{n} \left(p_{1j}\, e^{\frac{it}{2}} + p_{j1}\, e^{-\frac{it}{2}} \right), \end{aligned} \tag{11}$$

and $E\,[(v_1 - \bar{v})^2]$ is the coefficient of $(it)^2/2!$ in the expansion of (11) in powers of t. Now

$$\begin{aligned} \prod_{j=2}^{n} \left(p_{1j}\, e^{\frac{it}{2}} + p_{j1}\, e^{-\frac{it}{2}} \right) &= \prod_{j=2}^{n} \left[\sum_{k=0}^{\infty} (p_{1j} + (-1)^k p_{j1}) \frac{(it)^k}{2^k k!} \right] \\ &= \prod_{j=2}^{n} \left[1 + (p_{1j} - p_{j1}) \frac{it}{2 \cdot 1!} + \frac{(it)^2}{2^2 \cdot 2!} + \cdots \right]. \end{aligned} \tag{12}$$

Let

$$g_{jk} = g(x_j, x_k) = p_{jk} - p_{kj}. \tag{13}$$

Multiplying out the product in (12) we obtain

$$\begin{aligned} E(e^{it(v_1-\bar{v})}) = 1 + \frac{it}{2\cdot 1!}\sum_{j=2}^{n} g_{1j} \\ + \frac{(it)^2}{2^2\cdot 2!}\left[n-1+\sum{}' g_{1j}g_{1k}\right] + \cdots, \end{aligned} \tag{14}$$

where $\sum'$ indicates summation over the $(n-1)(n-2)$ terms with $j, k = 2, 3, \cdots, n$ and $j \neq k$. Then for fixed x_j,

$$E(v_1 - \bar{v})^2 = \tfrac{1}{4}\left[n - 1 + \sum{}' g_{1j}g_{1k}\right]. \tag{15}$$

Since the x_j are actually distributed according to the distribution function $F(x_j)$, we have

$$\begin{aligned} &E(e^{it(v_1-\bar{v})}) \\ &= \int\left[\prod_{j=2}^{n}\left(p_{1j}e^{\frac{it}{2}} + p_{j1}e^{-\frac{it}{2}}\right)\right] dF(x_1)\,dF(x_2)\cdots dF(x_n) \end{aligned} \tag{16}$$

where the integral is the Lebesque-Stieltjes integral and the integration is over the range of the x_j. Then, as in (15),

$$\begin{aligned} E[(v_1-\bar{v})^2] &= \tfrac{1}{4}\int\left[n-1+\sum{}' g_{1j}g_{1k}\right] dF(x_1)\,dF(x_2)\cdots dF(x_n) \\ &= \frac{(n-1)}{4}\left\{1 + (n-2)\int\left[\int g_{1j}\,dF(x_j)\right]^2 dF(x_1)\right\}. \end{aligned} \tag{17}$$

Finally using (7) and putting

$$A(x) = \int g(x, y)\,dF(y), \tag{18}$$

$$E(h) = \frac{3}{n+1}\left[1 + (n-2)\int A^2(x)\,dF(x)\right]. \tag{19}$$

Some applications of this formula and some of the conclusions which can be drawn from it are discussed in Sections 6 and 7 below.

5. VARIANCE OF h. The variance of h, $\sigma^2(h)$, may be similarly obtained by use of the characteristic function. The calculation is more involved and the general result is rather complicated. We shall only outline the steps and state the final formula as follows:

$$\sigma^2(h) = E(h^2) - E^2(h) = \left(\frac{12}{n^3-n}\right)^2 E\left[\left(\sum_{j=1}^{n}(v_j-\bar{v})^2\right)^2\right] - E^2(h)$$

$$= \left(\frac{12}{n^3-n}\right)^2 \left\{\sum_{j=1}^{n} E\left[(v_j-\bar{v})^4\right] + \sum_{\substack{j,k=1\\ j\neq k}}^{n} E\left[(v_j-\bar{v})^2(v_k-\bar{v})^2\right]\right\} \tag{20}$$

$$- E^2(h) =$$

$$\left(\frac{12}{n^3-n}\right)^2 \left\{ n \left[E(v_1-\bar{v})^4\right] + n(n-1)E\left[(v_1-\bar{v})^2(v_2-\bar{v})^2\right]\right\}$$

$$- E^2(h).$$

The quantity $E[(v_1 - v)^4]$ is given by the coefficient of $(it)^4/4!$ in the expansion of $E(e^{it(v_1-\bar{v})})$ in (16). This gives

$$E[(v_1-\bar{v})^4] = \frac{n-1}{16}\Big[3n - 5 + 2(3n-7)(n-2)\int A^2(x)\,dF(x)$$

$$+ (n-2)_{(3)}\int A^4(x)\,dF(x)\Big], \tag{21}$$

where

$$n_{(r)} = n(n-1)\cdots\cdots(n-r+1). \tag{22}$$

Similarly $E\,[(v_1 - \bar{v})^2(v_2 - \bar{v})^2]$ is obtained from the expansion of the characteristic function of $v_1 - \bar{v}$ and $v_2 - \bar{v}$:

$$E(e^{it_1(v_1-\bar{v})+it_2(v_2-\bar{v})}) = \int\left[\prod_{j=2}^{n}\left(p_{1j}\,e^{\frac{it_1}{2}} + p_{j1}\,e^{-\frac{it_1}{2}}\right)\right]$$

$$\cdot\left[\prod_{k=3}^{n}\left(p_{2k}\,e^{\frac{it_2}{2}} + p_{k2}\,e^{-\frac{it_2}{2}}\right)\right] dF(x_1)\,dF(x_2)\cdots\cdots dF(x_n), \tag{23}$$

which gives

$$E[(v_1-\bar{v})^2(v_2-\bar{v})^2]$$

$$= \tfrac{1}{16}\Big\{(n-1)^2 + 2(n-2)(n^2-2n-1)$$

$$\cdot\int A^2(x)\,dF(x) + 2(n-2)_{(2)}\int\int\Big\{4g(x,y)A(y) \tag{24}$$

$$+ 2(n-4)A(x)[A(x)+A(y)] + B(x,y)\Big\}$$

$$\cdot B(x,y)\,dF(x)\,dF(y) + (n-2)_{(4)}\left[\int A^2(x)\,dF(x)\right]^2\Big\},$$

where we have put

$$B(x,y) = \int g(x,z)g(y,z)\,dF(z). \tag{25}$$

Then from (20) we finally have

$$\begin{aligned}\sigma^2(h) = \frac{18(n-2)}{(n+1)(n+1)_{(3)}} \Bigg\{ & 1 + 2(n-4)\int A^2(x)\,dF(x) \\ & - \frac{3}{2}(3n^2 - 15n + 20)\left[\int A^2(x)\,dF(x)\right]^2 + \frac{(n-3)_{(2)}}{2} \\ & \cdot \int A^4(x)\,dF(x) + (n-3)\int\int\Big\{4g(x,y)A(y) \\ & + 2(n-4)A(x)[A(x)+A(y)] + B(x,y)\Big\} \\ & \cdot B(x,y)\,dF(x)\,dF(y)\Bigg\}.\end{aligned} \tag{26}$$

This formula is too complicated to be very useful but we can point out two simple cases.

If $p_{jk} = 1/2$ for all j and k, that is, for any pair of members the probability of the dominance relation going in either direction is the same; then $g_{jk} = 0$ and all the integrals in (26) vanish so that

$$\sigma^2(h) = \frac{18(n-2)}{(n+1)(n+1)_{(3)}} \sim 18/n^3. \tag{27}$$

In general, when the integrals do not vanish we have

$$\sigma^2(h) = O(1/n), \tag{28}$$

that is, $n\sigma^2(h) \to$ constant, as $n \to \infty$.

6. APPLICATIONS. *No Dominance Bias.* This case, with equal probability of dominance in either direction for every pair, $p_{jk} = \frac{1}{2}$ for all j and k, occurs if the x_j are all equal, that is, when every member of the society has the same ability. We then have $g_{jk} = 0$ and

$$E(h) = \frac{3}{n+1}. \tag{29}$$

As soon as n becomes moderately large, $E(h)$ becomes small and $E(h) \rightarrow 0$ as $n \rightarrow \infty$. Remembering that $0 \leq h \leq 1$, it follows, using the generalized Chebychev inequality (Cramér, 1946, p. 182), that the probability that h will differ very much from zero becomes very small as n increases. Among these societies equality rather than hierarchy would be the rule.

This then gives for general n the behavior of societies without bias toward dominance, which was given in detail for $n = 3, 4, 5$ by Rapoport (1949a). We also give a table of the distribution of V for $n = 6$. This was computed by induction from Rapoport's Table 2

DISTRIBUTION OF V FOR $n = 6$, $p_{jk} = \frac{1}{2}$

V	2^{15} . Probability of V	$35h$
(5, 4, 3, 2, 1, 0)	720	35
(5, 4, 3, 1, 1, 1)	240	31
(5, 4, 2, 2, 2, 0)	240	31
(5, 3, 3, 3, 1, 0)	240	31
(4, 4, 4, 2, 1, 0)	240	31
(5, 4, 2, 2, 1, 1)	720	27
(5, 3, 3, 2, 2, 0)	720	27
(4, 4, 4, 1, 1, 1)	80	27
(4, 4, 3, 3, 1, 0)	720	27
(5, 3, 3, 2, 1, 1)	1440	23
(4, 4, 3, 2, 2, 0)	1440	23
(5, 3, 2, 2, 2, 1)	1680	19
(4, 4, 3, 2, 1, 1)	2880	19
(4, 3, 3, 3, 2, 0)	1680	19
(5, 2, 2, 2, 2, 2)	144	15
(4, 4, 2, 2, 2, 1)	1680	15
(4, 3, 3, 3, 1, 1)	1680	15
(3, 3, 3, 3, 3, 0)	144	15
(4, 3, 3, 2, 2, 1)	8640	11
(4, 3, 2, 2, 2, 2)	2400	7
(3, 3, 3, 3, 2, 1)	2400	7
(3, 3, 3, 2, 2, 2)	2640	3

$E(h) = 3/7$

$\sigma^2(h) = 12/245$

(*loc. cit.*), using the fact that the probability of $V = (v_1, v_2, \cdots v_n)$ is the sum of the coefficients of terms of the form $t_{j_1}^{v_1} t_{j_2}^{v_2} \cdots t_{j_n}^{v_n}$ in the expansion of

$$\prod_{\substack{j,k=1\\ j\neq k}}^{n} (t_j + t_k).$$

Suppose $p_{jk} \neq 1/2$ for some j and k, that is, there are differences in ability making for biases toward dominance. Then it can be seen from equation (19) that $E(h)$ will be increased over its value in the unbiased case; a society tends to move from equality toward hierarchy when any bias is introduced. This was suggested by Rapoport, based on $n = 3$. We now determine $E(h)$ for some assumed forms of p_{jk} and $F(x)$.

Dominance Strictly Determined. At the opposite extreme from absence of any bias toward dominance, we might consider the case in which dominance is completely determined by any difference in ability, that is, we assume that the ability vector has a single component and that

$$\begin{aligned} p_{jk} &= 1 \quad \text{for } x_j > x_k, \\ &= 0 \quad \text{for } x_j < x_k, \end{aligned} \tag{30}$$

and we also assume that $F(x)$ is continuous, so that $Pr(x_j = x_k) = 0$. It is clear that in this case the only possible structure for the society is the hierarchy, but it is interesting to see how this follows from the formula for $E(h)$.

We have

$$\begin{aligned} g_{jk} &= 1 \quad \text{for } x_j > x_k, \\ &= -1 \quad \text{for } x_j < x_k; \end{aligned}$$

then

$$\begin{aligned} A(x_j) &= \int_{-\infty}^{x_j} dF(x_k) - \int_{x_j}^{\infty} dF(x_k) \\ &= F(x_j) - [1 - F(x_j)] = 2F(x_j) - 1, \end{aligned}$$

and

$$\int_{-\infty}^{\infty} A^2(x)\,dF(x) = \int_{-\infty}^{\infty} [4F^2(x) - 4F(x) + 1]\,dF(x) = \tfrac{1}{3};$$

so from (19)

$$E(h) = 1; \tag{31}$$

and since $h \leq 1$, then $h = 1$, or the hierarchy, is the only possible structure. From (26) we can also obtain $\sigma^2(h) = 0$ for this case.

Linear Dominance Probability. Suppose the probability of dominance depends linearly on the ability vector. This requires that the range of values of the ability factors be bounded. Let

$$x_j = (x_{ja}) = (x_{j1}, x_{j2}, \cdots, x_{jm}),$$

with $0 \le x_{ja} \le b_a$. Using the notation

$$\begin{aligned} S(x) &= 0, & x &< 0 \\ &= x, & 0 &\le x \le 1 \\ &= 1, & x &> 1, \end{aligned} \tag{32}$$

we put

$$p_{jk} = \sum_{a=1}^{m} w_a S\left(\frac{x_{ja} - x_{ka} + b_a}{2b_a}\right), \quad \text{with } w_a \ge 0, \sum w_a = 1, \tag{33}$$

so that p_{jk} is a weighted sum of linear functions of $x_{ja} - x_{ka}$ with w_a as weights.

Then

$$g_{jk} = \sum_{a=1}^{m} \frac{w_a}{b_a}(x_{ja} - x_{ka}), \quad \text{for } 0 \le x_{ja}, x_{ka} \le b_a,$$

and

$$\begin{aligned} A(x_j) &= \int_0^{b_m} \cdots \int_0^{b_1} \sum_{a=1}^{m} \frac{w_a}{b_a}(x_{ja} - x_{ka})\, dF(x_{k1}, \cdots, x_{km}) \\ &= \sum_{a=1}^{m} \frac{w_a}{b_a}(x_{ja} - \xi_a), \end{aligned}$$

where ξ_a is the mean of x_{ka}.

$$\begin{aligned} \int A^2(x_j)\, dF(x_j) &= \int_0^{b_m} \cdots \int_0^{b_1} \left[\sum_{a=1}^{m} \frac{w_a}{b_a}(x_{ja} - \xi_a)\right]^2 \\ &\quad \cdot dF(x_{j1}, \cdots, x_{jm}) \\ &= \sum_{a=1}^{m} \left(\frac{w_a}{b_a}\sigma_a\right)^2 + \sum_{\substack{a,\beta=1 \\ a \ne \beta}}^{m} \frac{w_a w_\beta \sigma_a \sigma_\beta}{b_a b_\beta} \rho_{a\beta}. \end{aligned} \tag{34}$$

where σ_a^2 = variance of x_{ja}, and $\rho_{a\beta}$ = correlation coefficient of x_{ja} and $x_{j\beta}$.

We could have chosen the x_{ja} to be uncorrelated, or transformed to uncorrelated variables. Assuming then $\rho_{a\beta} = 0$ we have

$$E(h) = \frac{3}{n+1}\left[1 + (n-2)\sum_{a=1}^{m}\left(\frac{w_a \sigma_a}{b_a}\right)^2\right] \sim 3\sum_{a=1}^{m}\left(\frac{w_a \sigma_a}{b_a}\right)^2. \quad (35)$$

In this case $E(h)$ has an upper bound which is less than one. Since $0 \leq x_{ja} \leq b_a$, we have $\sigma_a^2 \leq b_a^2/4$, so that, using (33),

$$E(h) \leq \frac{3}{n+1}\left[1 + \frac{n-2}{4}\sum_{a=1}^{m} w_a^2\right] \leq \frac{3}{4}\left(\frac{n+2}{n+1}\right). \quad (36)$$

This result indicates that in this case also the hierarchy will not be the usual structure, but structures far from equality may frequently occur. For rectangular distributions of the x_{ja}, we have

$$E(h) \leq \frac{1}{4}\left(\frac{n+2}{n+1}\right);$$

which is not far from equality.

If the number of factors, m, becomes large, while none of the weights, w_a, approaches zero, then $E(h)$ will become small. Thus for equal weights

$$w_1 = w_2 = \cdots = w_m = \frac{1}{m},$$

$$E(h) \leq \frac{3}{4m}\left(\frac{n+4m}{n+1}\right) \to 0, \quad \text{as } m \to \infty, \quad n \to \infty,$$

so that if there are a large number of significant factors in the ability vector the structure approaches the equality.

Normal Distribution. We now suppose that the factors of the ability vector are each normally distributed and uncorrelated, and that the probability of dominance is a weighted sum of normal probability integrals of the differences of the factors. Using the notation

$$G(x) = \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{x} e^{-\frac{t^2}{2}}\,dt$$

for the normal probability integral, we put

$$p_{jk} = \sum_{a=1}^{m} w_a\, G\left(\frac{x_{ja} - x_{ka}}{s_a}\right), \quad \text{with } w_a \geq 0, \sum_{a=1}^{m} w_a = 1, \quad (37)$$

and

$$F(x_j) = \prod_{a=1}^{m} G\left(\frac{x_{ja}}{\sigma_a}\right). \quad (38)$$

Then

$$g_{jk}=\sum_{\alpha=1}^{\infty} w_\alpha\left[\,2G\left(\frac{x_{j\alpha}-x_{k\alpha}}{s_\alpha}\right)-1\right]=-1+2\sum_{\alpha=1}^{m} w_\alpha\, G\left(\frac{x_{j\alpha}-x_{k\alpha}}{s_\alpha}\right)$$

and

$$A(x_j)=\int_{-\infty}^{\infty}\cdots\int_{-\infty}^{\infty}\left[-1+2\sum_{\alpha=1}^{m} w_\alpha\, G\left(\frac{x_{j\alpha}-x_{k\alpha}}{s_\alpha}\right)\right]\prod_{\alpha=1}^{m} dG\left(\frac{x_{k\alpha}}{\sigma_\alpha}\right)$$
$$=-1+2\sum_{\alpha=1}^{m} w_\alpha\, G\left(\frac{x_{j\alpha}}{\sqrt{s_\alpha^2+\sigma_\alpha^2}}\right),$$

using

$$\int_{-\infty}^{\infty} G(ax+b)\,dG(x)=G\left(\frac{b}{\sqrt{1+a^2}}\right),\quad \text{(Landau, 1950)}.$$

Then

$$\int A^2(x_j)\,dF(x_j)=\int_{-\infty}^{\infty}\cdots\int_{-\infty}^{\infty}\left[1-4\sum_{\alpha=1}^{m} w_\alpha\, G\left(\frac{x_{j\alpha}}{\sqrt{s_\alpha^2+\sigma_\alpha^2}}\right)\right.$$
$$+4\sum_{\alpha=1}^{m} w_\alpha^2\, G^2\left(\frac{x_{j\alpha}}{\sqrt{s_\alpha^2+\sigma_\alpha^2}}\right)+4\sum_{\substack{\alpha,\beta=1\\ \alpha\neq\beta}}^{m} w_\alpha w_\beta\, G\left(\frac{x_{j\alpha}}{\sqrt{s_\alpha^2+\sigma_\alpha^2}}\right) \tag{39}$$
$$\left.\cdot\, G\left(\frac{x_{j\beta}}{\sqrt{s_\beta^2+\sigma_\beta^2}}\right)\right]\prod_{\alpha=1}^{m} dG\left(\frac{x_{j\alpha}}{\sigma_\alpha}\right).$$

Using a method similar to that for $\int_{-\infty}^{\infty} G(ax+b)\,dG(x)$, it can be shown that

$$\int_{-\infty}^{\infty} G^2(ax)\,dG(x)=\frac{1}{4}+\frac{1}{2\pi}\arcsin\left(\frac{a^2}{1+a^2}\right).$$

Then (39) becomes

$$\begin{aligned}
&\int A^2(x_j)\,dF(x_j) \\
&= 1 - 2\sum_{\alpha=1}^{m} w_\alpha + 4\sum_{\alpha=1}^{m} w_\alpha^2 \left[\frac{1}{4} + \frac{1}{2\pi} \arcsin\left(\frac{\sigma_\alpha^2}{s_\alpha^2 + 2\,\sigma_\alpha^2} \right) \right] \\
&+ 4 \sum{}' w_\alpha w_\beta = 1 - 2\sum_{\alpha=1}^{m} w_\alpha \\
&+ \left(\sum_{\alpha=1}^{m} w_\alpha \right)^2 + \frac{2}{\pi} \sum_{\alpha=1}^{m} w_\alpha^2 \arcsin\left(\frac{\sigma_\alpha^2}{s_\alpha^2 + 2\,\sigma_\alpha^2} \right) \\
&= \frac{2}{\pi} \sum_{\alpha=1}^{m} w_\alpha^2 \arcsin\left(\frac{\sigma_\alpha^2}{s_\alpha^2 + 2\,\sigma_\alpha^2} \right), \quad \text{using } \sum_{\alpha=1}^{m} w_\alpha = 1,
\end{aligned} \tag{40}$$

and

$$E(h) = \frac{3}{n+1} \left[1 + \frac{2(n-2)}{\pi} \sum_{\alpha=1}^{m} w_\alpha^2 \arcsin\left(\frac{\sigma_\alpha^2}{s_\alpha^2 + 2\,\sigma_\alpha^2} \right) \right]. \tag{41}$$

The unbiased and strictly determined cases (29) and (31) can be obtained as limits from (41). For the unbiased case let $s_\alpha \to \infty$, then $p_{jk} \to \frac{1}{2}$, and

$$\arcsin\left(\frac{\sigma_\alpha^2}{s_\alpha^2 + 2\,\sigma_\alpha^2} \right) \to 0,$$

so

$$E(h) \to \frac{3}{n+1}.$$

For the strictly determined case take $m = 1$ and let $s_\alpha \to 0$, then $p_{jk} \to$ equation (30) and

$$\arcsin\left(\frac{\sigma_\alpha^2}{s_\alpha^2 + 2\,\sigma_\alpha^2} \right) \to \frac{\pi}{6},$$

so $E(h) \to 1$.

Here, as in the previous case, it can be seen from (41) that increasing the number of factors in the ability vector tends to reduce $E(h)$. When the number of significant factors determining dominance becomes large, the structure of the society moves toward equality.

7. SIGNIFICANCE FOR FLOCKS OF HENS. The observations and experiments on flocks of hens by Schjelderup-Ebbe and by Allee and

coworkers all show that stable flocks of hens almost always have a structure that departs very little from the hierarchy. A flock of ten to twenty hens will normally have not more than two or three cycles, i.e., $j > k$, $k > l$ and $l > j$. This means that h is normally very close to unity in such a flock. A typical example quoted by Schjelderup-Ebbe is the following score structure for a flock of ten hens: $V = (8, 8, 8, 6, 5, 4, 3, 2, 1, 0)$. This gives $h = .975$.

We wish to show that if the probability of dominance depended only on inherent individual characteristics as assumed in the present treatment (and not on social factors), then the occurrence of societies with h near one would be unusual rather than the rule.

We use the results for the normal distribution (Sec. 6) as being probably closest to reality. As noted in Section 6, if the ability vector contains several uncorrelated factors this will tend to reduce the expected value of h, so that we can consider the case of a single factor. Then

$$E(h) = \frac{3}{n+1} + \frac{n-2}{n+1} h_a,$$

where

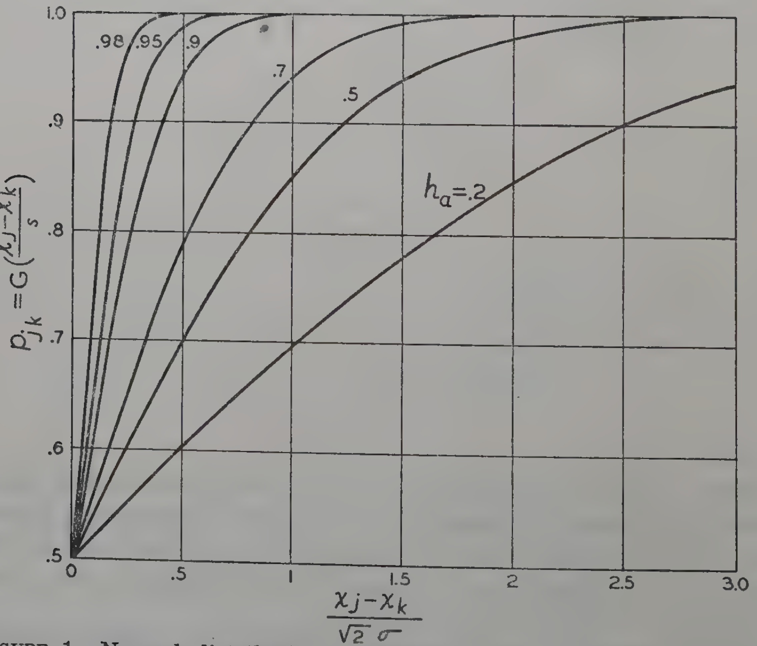

FIGURE 1. Normal distribution. Dependence of probability of dominance, p_{jk}, on difference in ability. Values on curves give h_a.

$$h_a = \frac{6}{\pi} \arcsin \frac{\sigma^2}{s^2 + 2\sigma^2}. \tag{42}$$

For even moderate n, $E(h)$ is close to h_a, its asymptotic value, and in any case

$$E(h) - h_a = \frac{3}{n-2}(1 - E(h)),$$

so we consider how h_a depends on s/σ.

In Figure 1 we have drawn the probability of dominance,

$$p_{jk} = G\left(\frac{x_j - x_k}{s}\right),$$

as a function of the difference in ability for various values of s/σ with the corresponding values of h_a noted on each curve. The abscissa is

$$\frac{x_j - x_k}{\sqrt{2}\,\sigma},$$

since the variance of $x_j - x_k$ is $2\,\sigma^2$. It can be seen that for h_a to be very close to one, very small differences in ability would have to be quite decisive as to dominance.

This very close dependence of dominance on ability hardly seems reasonable, but there is also some experimental evidence on this point. Collias (1943) staged 200 combats between hens in which he measured degree of moult, comb size, weight and rank in own flock, and obtained for the correlation with success the values: .580, .593, .474, and .262. The correlation measure used was Pearson's coefficient of biserial correlation, r, (Pearson, 1909) except for degree of moult which was not measured on a continuous scale. In the present case

$$r = \sqrt{\frac{\pi}{2}}\,\frac{\overline{x_1 - x_2}}{\sigma_{x_1 - x_2}}, \tag{43}$$

where $\overline{x_1 - x_2}$ is the mean of $x_1 - x_2$ when $x_1 > x_2$, and $\sigma_{x_1 - x_2}$ is the standard deviation of $x_1 - x_2$. It is not difficult to determine the value of r in terms of s/σ for our assumed normal distribution. The result is

$$r = \left(1 + \frac{s^2}{2\sigma^2}\right)^{-\frac{1}{2}}, \tag{44}$$

and this gives

$$h_a = \frac{6}{\pi} \arcsin \frac{r^2}{2}. \tag{45}$$

Hence the largest value of r obtained by Collias, .593, gives only $h_a = .34$. Figure 2 shows the dependence of h_a on r. It is apparent that h_a close to one requires r to be unreasonably large.

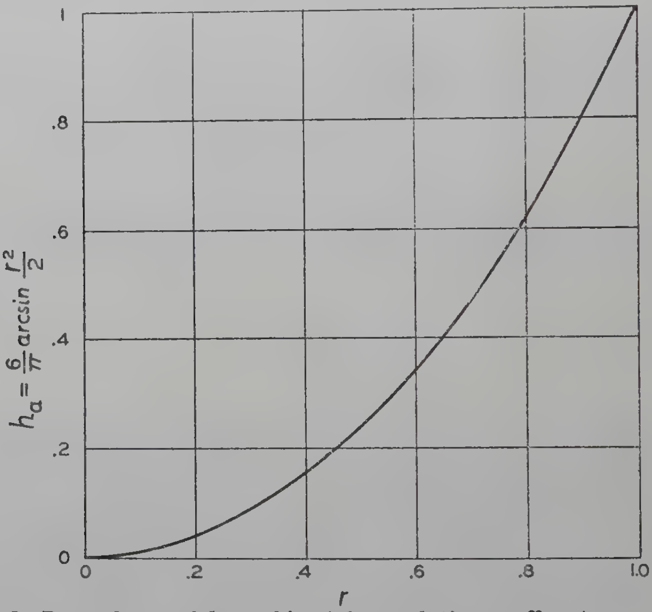

FIGURE 2. Dependence of h_a on biserial correlation coefficent, r.

We must conclude that factors omitted from the present treatment must be included to account for the observed frequency of structures near the hierarchy in flocks of hens. The most obvious omissions are the social factors, such as social lag, or the effect of existing differences in social rank on the probability of continued dominance. All observers agree that such social factors are of great importance. An attempt will be made to treat them mathematically in a later communication.

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A NOTE ON THE McCULLOCH-PITTS NEURAL NET FOR HEAT-COLD DISCRIMINATION

HERMAN T. EPSTEIN AND ANATOL RAPOPORT
THE UNIVERSITY OF PITTSBURGH† AND COMMITTEE ON MATHEMATICAL BIOLOGY,
THE UNIVERSITY OF CHICAGO

An error is pointed out in the neural net model which had been previously proposed to explain the heat-cold responses that depended on the duration of the stimulus. A corrected net for the effect is given.

In their paper on the Boolian algebra of neural nets, W. S. McCulloch and W. Pitts (1943) gave as an illustration a neural net which was to satisfy the following physiological situation:

a) When a cold object momentarily touches the skin, a sensation of heat develops;

b) When the cold object is held on the skin for a longer time, the sensation is one of cold, with no accompanying sensation of heat.

The authors derived the circuit of Figure 1 to represent the above situation.

The simultaneous firing of two end-feet is required to fire the neuron on which they synapse. That is, for example, the neuron N_4 will fire provided N_a fires one time interval previously and simultaneously N_2 fires one time interval previously. In the notation of N. Rashevsky (1948) this is expressed as

$$N_4(t) \equiv N_a(t-1) \cdot N_2(t-1). \tag{1}$$

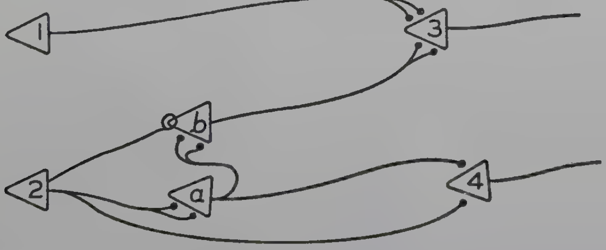

FIGURE 1

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†Contribution no. 3 of the Department of Biophysics of the University of Pittsburgh.

The looping connection of N_2 on N_b is one of complete inhibition. If N_2 fires at any time, then N_b will not fire at one time interval later, no matter what its other stimulations may be. The circuit of Figure 1 was derived to fit the equations,

$$N_4(t) \mathrel{.{\equiv}.} N_2(t-1) \cdot N_2(t-2) \tag{2}$$

$$N_3(t) \mathrel{.{\equiv}.} N_1(t-1) \vee [N_2(t-3) \cdot \overline{N_2(t-2)}], \tag{3}$$

where N_1 is the receptor for heat, N_2 the receptor for cold, N_3 the neuron which leads to centers giving a sensation of heat, and N_4 correspondingly leads to a sensation of cold.

The purpose of the present note is to point out that the circuit does not satisfy the condition that there be no sensation of heat if the cold object is held on the skin for more than one time interval. This is so, because when N_2 *stops* firing, say at $(t + k)$, N_a still fires at $(t + k)$, and, since N_b is now not inhibited by N_2, N_b fires at $(t + k + 1)$ and N_3 (the heat neuron) fires at $(t + k + 2)$.

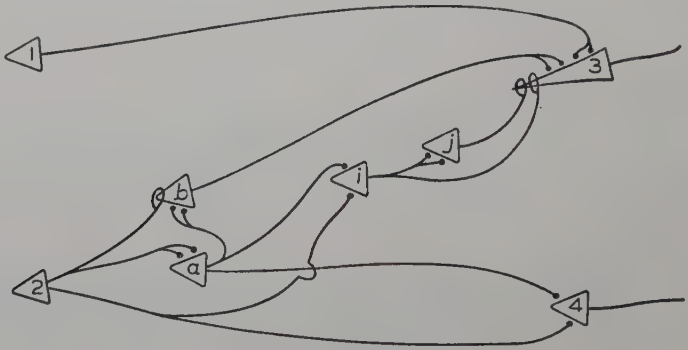

FIGURE 2

The net in Figure 2 is proposed as realizing conditions a) and b) above where b) is strengthened to

b′) When the cold object is held on the skin for a longer time, the sensation is one of cold, with no sensation of heat either preceding or following.

The inhibitory connections from N_i and N_j prevent the firing of N_3 by N_2 at all times, except when N_2 fires exactly once, as can be readily verified.

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A NOTE ON THE EQUATIONS OF CONDITIONED REFLEX

JOHN Z. HEARON
DEPARTMENT OF PHYSIOLOGY
THE UNIVERSITY OF CHICAGO

An alternative method is suggested for integrating a certain differential equation associated with a conditioning process, where the stimulus is presented in the form of a "square wave," i.e., is of constant intensity during an interval of time followed by no stimulus during the next interval, etc.

A solution is also given where the stimulus is a rectified sine wave.

In discussing a simple, illustrative case of conditioning based on the two-factor theory N. Rashevsky considers that the conditioned and unconditioned stimuli are presented together at regular intervals. The excitatory factor, ε, then obeys the equation

$$\frac{d\varepsilon(t)}{dt} = AE(t) - a\varepsilon(t) \tag{1}$$

wherein the total intensity of excitation, $E(t)$ has, beginning at $t=0$, the value E for an interval t_1, is then zero for an interval t_2, then has the value E for an interval t_1, etc.

The solution of equation (1) under the above conditions on $E(t)$ was obtained by Rashevsky essentially as follows: The integral of (1) with $E(t) = E$ describes $\varepsilon(t)$ during a t_1-interval. During a t_2-interval $\varepsilon(t)$ is described by the integral of the equation

$$\frac{d\varepsilon(t)}{dt} = -a\varepsilon(t) \tag{2}$$

which gives the decay of ε when $E(t) = 0$. For any period the *initial* conditions are given by the *terminal* conditions of the preceding period. By piece-wise integration in this manner the conditions for an induction are set up: It is shown that if the formula obtained for ε at the end of the second t_1-period is true when generalized for the nth t_1-period it is then true for the $(n + 1)$st t_1-period. The general formula for ε at the end of the nth t_1-period is thereby established.

The biophysical limitations of the simple theory of conditioning which gave rise to the above problem as well as the modifications and extensions which make it more realistic have been discussed by N. Rashevsky (1948, p. 436–42).

It is the purpose of this note to discuss the purely mathematical point that the straightforward integration of (1), subject to the above described conditions on $E(t)$, leads at once to the general result given by Rashevsky. The increase in ε when $E(t) = E$ and the decay of ε when $E(t) = 0$ are *automatically* accounted for in the method here described.

The solution of (1), when $\varepsilon(0) = 0$, is

$$\varepsilon(t) = A \int_0^t e^{-a(t-\lambda)} E(\lambda)\, d\lambda = A \int_0^t e^{-a\lambda} E(t-\lambda)\, d\lambda . \tag{3}$$

For the purpose of illustration consider $E(t)$ to be the half-wave rectification of the square wave of amplitude E and period $2c$. Of the two quadratures indicated in (3) the second is simpler to perform; the first more clearly exhibits the features of the general method. The first quadrature in (3) gives for ε at the end of n half periods:

$$\varepsilon(nc) = A\,E \sum_{k=0}^{\xi} \int_{2kc}^{(2k+1)c} e^{-a(nc-\lambda)}\, d\lambda \tag{4}$$

where ξ, the upper index of the summation is

$\xi = (n-1)/2$ when n is odd,
$\xi = (n-2)/2$ when n is even.

When the integrations indicated in (4) are carried out the result is

$$\varepsilon(nc) = \frac{A\,E}{a}(1 - e^{-ac}) \sum_{k=0}^{\xi} e^{-a(n-1-2k)c}. \tag{5}$$

When k takes on the values $0, 1, 2, \cdots (n-1)/2$ the quantity $(n-1-2k)$ takes on the values $(n-1), (n-3), (n-5), \cdots, 0$. When k takes on the values $0, 1, 2, \cdots, (n-2)/2$ the quantity $(n-1-2k)$ takes on the values $(n-1), (n-3), (n-5), \cdots, 1$. A simple change of index then gives

$$\varepsilon(nc) = \frac{A\,E}{a}(1 - e^{-ac}) \sum_{i=0}^{(n-1)/2} e^{-i2ac}; \quad n \text{ odd} \tag{6}$$

and

$$\varepsilon(nc) = \frac{AE}{a}(1 - e^{-ac})e^{-ac} \sum_{i=0}^{(n-2)/2} e^{-i2ac}; \quad n \text{ even.} \tag{7}$$

The summations in equations (6) and (7) are the sum of $(n+1)/2$ and $n/2$ terms respectively of the geometric progression of common ratio e^{-2ac}. Equations (6) and (7) thus become

$$\varepsilon(nc) = \frac{AE}{a}(1 - e^{-ac}) \frac{1 - e^{-\frac{(n+1)}{2} \cdot 2ac}}{1 - e^{-2ac}}; \quad n \text{ odd} \tag{8}$$

and

$$\varepsilon(nc) = \frac{AE}{a}(1 - e^{-ac}) \frac{1 - e^{-\frac{n}{2} \cdot 2ac}}{1 - e^{-2ac}} e^{-ac}; \quad n \text{ even.} \tag{9}$$

When n is odd $\varepsilon(nc)$, the value of ε at the end of n half periods, is also the value of ε at the end of $(n+1)/2$ "stimulatory periods" [intervals during which $E(t) = E$]. When n is even $\varepsilon(nc)$ is the value of ε at the end of $n/2$ "rest periods" [intervals during which $E(t) = 0$]. Thus (8) or (9) gives ε directly in terms of the number of stimulatory periods or rest periods when the *total* time interval terminates with a stimulatory or rest period. It is also clear that if m is an odd integer then, from (8) and (9),

$$\varepsilon([m+1]c) = \varepsilon(mc)e^{-ac}, \tag{10}$$

the physical interpretation of which is quite apparent.

When $E(t)$ has the form

$$\begin{aligned} E(t) &= E, \quad n(t_1 + t_2) \leq t \leq (n+1)t_1 + nt_2 \\ &= 0, \quad (n+1)t_1 + nt_2 < t < (n+1)(t_1 + t_2) \\ &\qquad n = 0, 1, 2, \cdots \end{aligned} \tag{11}$$

equation (3) gives for ε at the end of the nth t_1-period

$$\varepsilon(nt_1 + [n-1]t_2) = AE \sum_{k=0}^{n-1} \int_{k(t_1+t_2)}^{(k+1)t_1+kt_2} e^{-a[nt_1+(n-1)t_2-\lambda]}\, d\lambda. \tag{12}$$

When the definite integrals in (12) are evaluated the result is

$$\begin{aligned} \varepsilon(nt_1 + [n-1]t_2) &= \frac{AE}{a}(1 - e^{-at_1}) \sum_{i=0}^{n-1} e^{-ia\tau} \\ &= \frac{AE}{a}(1 - e^{-at_1}) \frac{1 - e^{-n.a\tau}}{1 - e^{-a\tau}}, \end{aligned} \tag{13}$$

where $\tau \equiv t_1+t_2$. In quite the same manner the value of ε at the end of the nth t_2-period is found to be

$$\varepsilon(nt_1+nt_2)=\frac{A\,E}{a}\,(1-e^{-at_1})\,e^{-at_2}\,\frac{1-e^{-n.a\tau}}{1-e^{-a\tau}}. \tag{14}$$

Equations (13) and (14) are identical with the results of Rashevsky (1948). They yield the physically obvious relation, equivalent to (10),

$$\varepsilon(nt_1+nt_2)=\varepsilon(nt_1+[n-1]t_2)\,e^{-at_2}. \tag{15}$$

When $t_1=t_2=c$, equations (8) and (9) are recovered from equations (13) and (14) respectively.

By the same general method two further results which are of possible interest may be readily obtained. Let $E(t)$ be given by

$$\begin{aligned} E(t) &= E\sin\omega t\,, && n(t_2+\pi/\omega)\le t\le nt_2+(n+1)\pi/\omega \\ &= 0\,, && nt_2+(n+1)\pi/\omega<t<(n+1)(t_2+\pi/\omega) \\ & && n=0,1,2,\cdots; \end{aligned} \tag{16}$$

the value of ε at the end of s stimulatory periods is found to be

$$\begin{aligned} &\varepsilon(s\pi/\omega+[s-1]t_2) \\ &\quad=\frac{A\,E\,\omega}{a^2+\omega^2}\sum_{k=0}^{s-1}e^{-a\beta(\pi/\omega+t_2)}\,[a\sin\alpha-\omega\cos\alpha] \\ &\quad\times[\cos(k+1)\pi-e^{-a\pi/\omega}\cos k\pi], \end{aligned} \tag{17}$$

where $\beta\equiv s-k-1$ and $\alpha\equiv k\omega t_2$.

If $t_2=\pi/\omega$ then (16) gives the half wave rectification of $E\sin\omega t$ and (17) becomes

$$\begin{aligned} \varepsilon([2s-1]\pi/\omega) &= \frac{A\,E\,\omega}{a^2+\omega^2}\sum_{i=0}^{s-1}(1+e^{-a\pi/\omega})\,e^{-i2a\pi/\omega} \\ &= \frac{A\,E\,\omega}{a^2+\omega^2}\,(1+e^{-a\pi/\omega})\,\frac{1-e^{-s.2a\pi/\omega}}{1-e^{-2\pi a/\omega}}. \end{aligned} \tag{18}$$

Since s stimulatory periods correspond to a total of $n=2s-1$ half periods, equation (18) with $s=(n+1)/2$ gives $\varepsilon(n\pi/\omega)$, the value of ε at the end of an odd number, n, of half periods.

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MATHEMATICAL BIOPHYSICS
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ON PERMEABILITY DETERMINATION OF THE ERYTHROCYTE

I. OPATOWSKI
COMMITTEE ON MATHEMATICAL BIOLOGY
THE UNIVERSITY OF CHICAGO

A procedure is indicated to test the assumptions underlying the theory of determination of the permeability coefficients of the erythrocyte from its volume changes.

A method for the determination of the permeability coefficients of the erythrocyte from its volume changes caused by the penetration of an isosmotic solution into the cell is well known. The differential equations which are encountered in that method are non-linear. M. H. Jacobs (1934), who developed the method, gave numerical tables for the solution of these equations. It is the purpose of this note to indicate a procedure for checking the assumptions involved in the theory of this method, for instance, the assumption of independence of the permeability coefficients on the solute concentration. E Schiödt (1933) has shown that a sufficient number of measurements can be carried out to represent the relation between the erythrocyte volume V and the duration of diffusion t by a smooth curve $V(t)$. The availability of such a smoothed relation is required for the application of the procedure here indicated.

Let us consider an erythrocyte surrounded by an isosmotic solution of a particular solvent. Let S_I be the number of solute molecules inside the cell at any time t and W_I the number of solvent molecules therein. Let $[S_I]$ $[S_E]$ $[W_I]$ $[W_E]$ be the concentrations of those substances inside and outside of the cell respectively expressed as number of molecules per cm^3. Let $[\sigma_I]$ be the concentration of other osmotically active substances inside the cell whose diffusion through the cell membrane is assumed to be negligible, so that their amount σ_I inside is constant. Let h_S and h_W be the permeability coefficients of the solute and of the solvent, and A the area of the erythrocyte. The definition of the permeability coefficient gives the following differential equations:

$$dS_I/dt = h_S A([S_E] - [S_I]), \tag{1}$$

$$dW_I/dt = h_W A([W_E] - [W_I]). \tag{2}$$

The particular shape of the erythrocyte makes it possible to assume that within the range of swelling considered the cell maintains its area constant (cf. Ponder, 1948, p. 82). This implies that the volume change of the cell is unaccompanied by changes in the stress of the cell membrane, which requires a constancy of the external and internal pressures during the process of diffusion. Consequently, assuming that the relationship between the pressure and the concentration is ruled by the law of perfect gases, we have:

$$[S_I] + [W_I] + [\sigma_I] = [S_E] + [W_E] = C = \text{constant}. \tag{3}$$

The experimental conditions are, in general, such that $[S_E]$ and $[W_E]$ can be considered individually also as constant. Then:

$$dV/dt = C^{-1} d(S_I + W_I + \sigma_I)/dt \approx (dW_I/dt)/C, \tag{4}$$

if we neglect the change of the amount of the solute with respect to that of the solvent. Substituting equation (4) in equation (2) and eliminating $[W_E]$ and $[W_I]$ by means of equation (3) we obtain

$$ds/dt = [1 - (s/v)]\,\sigma, \tag{5}$$

$$dv/dt = [(s+1)/v - 1]\,\omega, \tag{6}$$

where

$$s = S_I/\sigma_I,\ v = [S_E]V/\sigma_I,\ \sigma = h_S A[S_E]/\sigma_I,\ \omega = h_W A[S_E]^2/(\sigma_I C).$$

Equations (5) and (6) are Jacobs' equations. An initial condition is $s(0) = 0$, i.e., no solute exists inside the cell at the beginning. With these conditions equations (5) and (6) can be written in the form:

$$s(t) = \sigma\, e^{-\sigma I(t)} \int_0^t e^{\sigma I(t)} dt = \frac{v}{\omega}\frac{dv}{dt} + v - 1, \tag{7}$$

where $I(t) = \int_0^t dt/v(t)$. Since ω is known from measurements on penetration of the pure solvent into the cell (cf. Jacobs, *loc cit.*) and $v(t)$ is known from the measured changes of the erythrocyte volume in the presence of the solution, all quantities in the middle and right-hand sides of equation (7) are numerically known, except σ. Thus the problem of finding σ is reduced to that of fitting a given curve $R(t)$ to a one-parametric equation

$$\sigma[J(t)]^{-\sigma} \int_0^t [J(t)]^{\sigma} \, dt = R(t) \qquad (8)$$

where R and J are known functions, R being the right-hand side of equation (7) and $J(t) = \exp [I(t)]$. A value of σ is obtainable from Jacobs' tables, and the difference between the two sides of equation (8) gives an indication as to the accuracy of the fit and the correctness of the assumptions underlying the theory. Equation (8) can be also used to determine σ.

This work was aided by a grant from the Dr. Wallace C. and Clara A. Abbott Memorial Fund of The University of Chicago.

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ON THE DIFFUSION OF METABOLIC INTERMEDIATES

A. T. Reid
Committee on Mathematical Biology
The University of Chicago

A simple model of diffusible metabolic intermediates, produced in a spherical cell, is postulated. The rate of production of the intermediate is taken to be a linear function of its internal concentration. The intermediate is produced by the degradation of some precursor substance at a rate which is assumed to decrease with increasing internal concentration. Assuming the medium in which the cell is enclosed to be infinite in extent, and the external concentration of the intermediate constant, the time dependent and steady-state solutions of the diffusion problem involved are obtained. It is shown that production of the intermediate will not cease, for any value of $r \leq r_0$, where r_0 is the radius of the cell. Possible application of this approach to the study of the occurrence of the lag phase in bacterial growth processes is indicated.

The elucidation of the rôle of diffusible metabolic intermediates in the overall activities of the metabolizing cell is of fundamental import in cellular biology. The studies of C. N. Hinshelwood (1946) on the kinetic aspects of bacterial growth have been concerned, in part, with the occurrence of the lag phase and the diffusion of certain essential intermediates. He views the duration of the lag phase as depending on the presence of a certain amount of the intermediate in the culture medium when a transfer is made from a growing culture to a new medium.

If we consider the phenomenon of lag as being due to a necessary readjustment in the metabolic processes of the organism that must occur before the organism can enter the logarithmic growth phase, then there may exist a relationship between the rate of a consecutive set of reactions taking place within the cell and the rate of change of the external and internal concentrations of some intermediate produced.

The mathematical biophysics approach to the problem of diffusion of metabolic intermediates will be to postulate certain metabolic models that exhibit different modes of intermediate production, and to examine these models for the relationships between internal and external concentrations of the intermediates, and the influence they have on the behavior of the metabolic model.

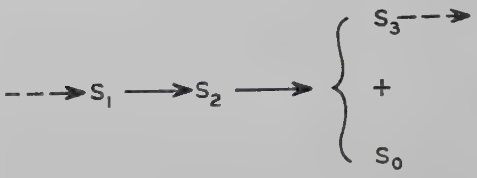

FIGURE 1

In this paper we will consider a simple model such as depicted in Figure 1. Consider a spherical metabolizing cell of radius r_0 in a medium of infinite extent. Let a simple reaction, such as shown above, be taking place where a precursor substance S_1 gives rise to another substance S_2. The substance S_2 is degraded in the next step of the reaction to give a substance S_3 and an intermediate which we will designate S_0. We will denote by c_i the internal concentration of the intermediate, and by c_j its external concentration.

Consider the general diffusion equation (Rashevsky, 1948)

$$D_i \nabla^2 c_i + q = \frac{\partial c_i}{\partial t}, \tag{1}$$

where D_i is the internal diffusion coefficient, c_i the internal concentration, and q the rate of production of the intermediate. Let us assume that

$$q = a - bc_i, \tag{2}$$

i.e., the rate of production is a linear function of the concentration, varying from a when none is present to zero when $c_i = a/b$.

The symmetry and homogeneity of the spherical cell indicate that the concentration c_i will be a function of t and the single space variable r, the distance from the center of the cell. In spherical coordinates equations (1) and (2) reduce to

$$D_i \left(\frac{\partial^2 c_i}{\partial r^2} + \frac{2}{r} \frac{\partial c_i}{\partial r} \right) + (a - bc_i) = \frac{\partial c_i}{\partial t}. \tag{3}$$

This partial differential equation holds within the cell.

The rate of flow Φ_b of the intermediate per unit area across the boundary of the cell, at $r = r_0$, is assumed to be proportional to $4\pi r_0^2 (c_i - c_j)$, thus

$$\Phi_b = 4\pi r_0^2 h (c_i - c_j),$$

where h is the permeability. Across any spherical shell of thickness Δr within the cell we expect the intermediate to diffuse at the rate $4\pi r_0^2 (\Delta c_i / \Delta r)$, or across any spherical surface,

$$\Phi_s = -4\pi r_0^2 D_i \left(\frac{\partial c_i}{\partial r} \right)_{r=r_0} .$$

But since the intermediate must be conserved, we have at the boundary

$$\Phi_b = \Phi_s ,$$

and so

$$h(c_i - c_j) = -D_i \left(\frac{\partial c_i}{\partial r} \right)_{r=r_0} . \tag{4}$$

Let us donate by c_0 the initial concentration of the intermediate within the cell and assume a constant outside concentration. In considering the external concentration to be constant we assume the medium to be well-stirred or the external diffusion coefficient $D_j = \infty$.

Solution of Problem. If we make the substitutions

$$v = rD_i^{-1}(a - bc_i)$$

and $\tau = D_i t$, the boundary value problem becomes

$$\frac{\partial^2 v}{\partial r^2} - \frac{b}{D_i} v = \frac{\partial v}{\partial \tau}, \tag{5}$$

with the conditions

$$\left. \frac{\partial v}{\partial r} \right)_{r=r_0} = G + Hv(r_0, \tau) , \tag{6}$$

and

$$v(r, 0) = \frac{r}{D_i} (a - bc_0) . \tag{7}$$

The additional condition

$$v(0, \tau) = 0 \tag{8}$$

arises from our definition of $v(r, \tau)$. In (6) we have used the constants

$$G = \frac{r_0 h}{D_i^2} (a - bc_j) , \quad H = \left(\frac{D_i - hr_0}{D_i r_0} \right) .$$

Now let

$$v(r, \tau) = w(r, \tau) + z(r) , \tag{9}$$

where

$$\frac{\partial^2 w}{\partial r^2} - \frac{b}{D_i} w = \frac{\partial w}{\partial \tau}, \tag{10}$$

and

$$\frac{d^2 z}{dr^2} - \frac{b}{D_i} z = 0. \tag{11}$$

Further, require that $z(0) = 0$, and

$$\left.\frac{dz}{dr}\right)_{r=r_0} = G + Hz(r);$$

while $w(r, \tau)$ satisfies the conditions

$$\left.\frac{\partial w}{\partial r}\right)_{r=r_0} = Hw(r_0, \tau), \tag{12}$$

and

$$w(0, \tau) = 0. \tag{13}$$

We see that

$$z(r) = \frac{G \sinh rk}{[k \cosh r_0 k - H \sinh r_0 k]}$$

satisfies the conditions imposed on z, and we now find from (7) and (9) that

$$w(r, 0) = \frac{r}{D_i}(a - bc_0) - \frac{G \sinh rk}{[k \cosh r_0 k - H \sinh r_0 n]}. \tag{14}$$

In the above expressions we made the substitution $k = \sqrt{\frac{b}{D_i}}$. Equations (10), (12), (13), and (14) constitute a boundary value problem in $w(r, \tau)$ which is to be solved.

Let

$$w(r, \tau) = R(r)T(\tau),$$

and substitute in (10), writing it in the form

$$\frac{R''}{R} = \frac{T'}{T} + k^2. \tag{15}$$

Since the function on the left can vary only with r and the one on the right only with τ, they must both equal a constant, say $-\lambda^2$. From (15) we have the two ordinary differential equations

$$R'' + \lambda^2 R = 0\,, \tag{16}$$

and

$$T' + (k^2 + \lambda^2)T = 0\,. \tag{17}$$

From (12) we find that

$$(R' - HR)_{r=r_0} = 0\,, \tag{18}$$

and from (13)

$$R(0) = 0\,. \tag{19}$$

The system (16), (18), and (19) has solutions

$$R(r) = E_n \sin \lambda_n r\,, \tag{20}$$

where $\lambda_n (n = 1, 2, 3 \cdots)$ are roots of the characteristic equation

$$\lambda_n = H \tan \lambda_n r_0\,. \tag{21}$$

Roots of this equation can be determined graphically, or found in mathematical tables (Jahnke and Emde, 1945).

Equation (17) has the solutions

$$T_n = F_n e^{-(k^2+\lambda_n^2)\tau}, \tag{22}$$

therefore the product

$$R_n T_n = w_n = K_n e^{-(k^2+\lambda_n^2)\tau} \sin \lambda_n r \tag{23}$$

satisfies all requirements for $w(r, \tau)$ except (14).

We now write

$$w(r, \tau) = \sum_{n=1}^{\infty} K_n e^{-(k^2+\lambda_n^2)\tau} \sin \lambda_n r\,,$$

and since the functions $\sin \lambda_n r$ are orthogonal in the interval $0 \leq r \leq r_0$ (Sommerfeld, 1949) we choose K_n as the Fourier coefficient in the series from $w(r, 0)$, as given by (14). Thus

$$w(r, 0) = \sum_{n=1}^{\infty} K_n \sin \lambda_n r\,,$$

and

$$K_n = \frac{4\lambda_n}{\{2\lambda_n r_0 - \sin 2\lambda_n r_0\}} \int_0^{r_0} w(r, 0) \sin \lambda_n r dr;$$

hence

$$K_n = \frac{4\lambda_n}{[2\lambda_n r_0 - \sin 2\lambda_n r_0]}\left\{\frac{(a-bc_0)}{D_i\,\lambda_n^2}(\sin\lambda_n r_0 - \lambda_n r_0\cos\lambda_n r_0) - \frac{G(k\sin\lambda_n r_0\cosh kr_0 - \lambda_n\sinh kr_0\cos\lambda_n r_0)}{(k^2+\lambda_n^2)(k\cosh kr_0 - H\sinh kr_0)}\right\}.$$

The solution, $c_i(r, t)$, can now be written

$$c_i(r, t) = \frac{a}{b} - \frac{D_i}{br}\sum_{n=1}^{\infty} K_n e^{-(b/D_i+\lambda_n^2)t}\sin\lambda_n r - \frac{Gd_i}{b\{k\cosh kr_0 - H\sinh kr_0\}}\times\frac{\sinh kr}{r}. \tag{24}$$

The Steady-state. From the time dependent solution we find that in the steady-state

$$c_i = \frac{a}{b} - \frac{hr_0^2(a-bc_j)}{b\{D_i r_0 k\cosh kr_0 - (D_i - hr_0)\sinh kr_0\}}\times\frac{\sinh kr}{r}. \tag{25}$$

We know from our definition of q as a function of c_i that if $c_i = a/b$ the intermediate will no longer be produced. Hence we are interested in determining if for any $r \leq r_0$ the internal concentration will equal the above value. If the second term on the right in (25) remains positive c_i will, for all values of $r \leq r_0$, be less than a/b. Consider the denominator of the coefficient of $(\sinh kr)/r$:

$$P(r_0) = b\{D_i r_0 k\cosh kr_0 - (D_i - hr_0)\sinh kr_0\}.$$

Let us rewrite $P(r_0)$ as follows:

$$P(r_0) = b\{D_i(kr_0\cosh kr_0 - \sinh kr_0) + hr_0\sinh kr_0\}.$$

Both $\sinh kr_0$ and $\cosh kr_0$ are monotonically increasing functions. The expression $kr_0\cosh kr_0 - \sinh kr_0$ is zero for $r_0 = 0$, and its derivative $k^2 r_0\sinh kr_0$ is positive everywhere. Hence $P(r_0)$ is always positive.

At the center of the cell, $r = 0$, we have

$$\sigma = \lim_{r\to 0} c_i = \frac{a}{b} - \frac{khr_0^2(a-bc_j)}{b\{D_i(kr_0\cosh kr_0 - \sinh kr_0) + hr_0\sinh kr_0\}}. \tag{26}$$

The distribution of the internal and external concentrations is the system shown in Figure 2.

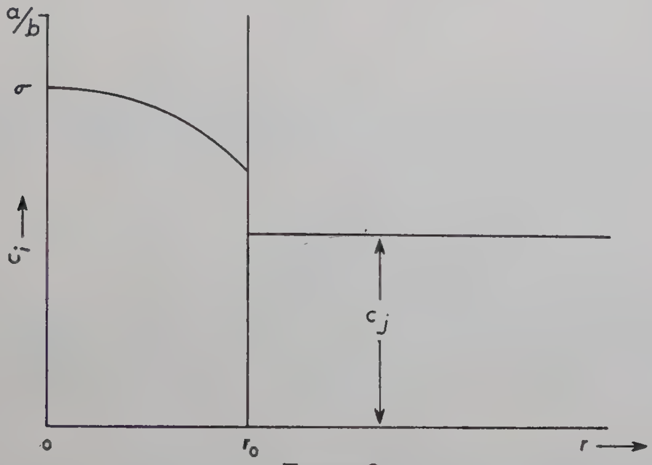

FIGURE 2

The application of this approach to chains of autocatalytic reactions and cyclic reactions is now being considered, with the hopes that it may be useful in the study of the rôle of diffusible metabolic intermediates in growth processes.

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A NOTE ON RAPOPORT'S APPROXIMATE FORMULA FOR THE INPUT-OUTPUT CURVE IN THE CASE OF BILATERAL PRE-INHIBITION

S. LEVINSOHN
COMMITTEE ON MATHEMATICAL BIOLOGY
THE UNIVERSITY OF CHICAGO

The accuracy of an approximation method used in a certain input-output problem of randomized stimuli is evaluated. The curves derived from it are shown to be close approximations to those derived by a statistically "exact" method.

A. Rapoport (1950) derives the following expression for the output of a neuron stimulated by two other neurons in the case of "bilateral pre-inhibition."

$$x_3 = \frac{2x(x\delta + 1)}{2x^2\delta^2 + 4x\delta + e^{-x\delta}}, \tag{1}$$

where x is the frequency of the outside (Poisson-randomized) input and x_3 the output of the neuron.

By an approximate method, Rapoport derives the expression

$$\bar{x}_3 = \frac{2x}{2x\delta + 1}. \tag{2}$$

To determine the maximum error obtained by working with $\bar{x}_3$ instead of with x_3, we can proceed as follows. Let $\bar{x}_3/x = R$. Then

$$R = 1 + \frac{x\delta + e^{-x\delta} - 1}{2x^2\delta^2 + 3x\delta + 1}. \tag{3}$$

Let $x\delta = y$; then

$$\begin{aligned} \frac{dR}{dy} &= R' \\ &= \frac{(2y^2 + 3y + 1)(1 - e^{-y}) - (y + e^{-y} - 1)(4y + 3)}{(2y^2 + 3y + 1)^2}. \end{aligned} \tag{4}$$

To find the values of y for which R is a maximum, we set $R' = 0$. Then

$$-2y^2 + 4y + 4 - e^{-y}(2y^2 + 7y + 4) = 0; \tag{5}$$

$$e^{-y} = \frac{-2y^2 + 4y + 4}{2y^2 + 7y + 4}. \tag{6}$$

Let

$$\frac{-2y^2 + 4y + 4}{2y^2 + 7y + 4} \equiv r.$$

At $y = 0$, $r = 1$, and $R = 1$ (a minimum value of R).

Likewise for $y = \infty$, $R = 1$. Calculation of r and e^{-y} to three decimal places gives us the following table:

y	r	e^{-y}
0.00	1.000	1.000
0.01	0.992	0.990
0.10	0.928	0.905
0.50	0.687	0.606
1.00	0.461	0.368
2.00	0.154	0.135
2.10	0.130	0.122
2.15	0.118	0.116
2.16	0.116	0.115
2.17	0.114	0.114
2.20	0.107	0.111

The maximum error in the use of the approximate formula occurs when $r = e^{-y}$, i.e., at $y = 2.17$. Then $R = \bar{x}_3/x_3 = 1.0759$. Thus the maximum error is seen not to exceed 8%.

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ON THE MATHEMATICAL THEORIES OF EXCITATION

I. Opatowski
Committee on Mathematical Biology
The University of Chicago

The question of constancy of the velocity of propagation of excitation is discussed on the basis of the two-factor theory, and differences between this and Blair's theory are examined.

The mathematical theories of excitation express the effect of a stimulus as the magnitude of a quantity, ε in Blair's theory, with

$$d\,\varepsilon/dt = \sigma I - \rho\,\varepsilon\,, \tag{1}$$

and $\varepsilon - j$ in Rashevsky's theory, with

$$\begin{cases} d\,\varepsilon/dt = \sigma_\varepsilon I - \rho_\varepsilon(\varepsilon - \varepsilon_0) \\ dj/dt = \sigma_j I - \rho_j(j - j_0)\,. \end{cases} \tag{2}$$

The σ's and ρ's are constants characterizing the biological system, t is the time, I the magnitude of the stimulus, the initial conditions being $\varepsilon(0) = 0$ for equation (1) and

$$\varepsilon(0) = \varepsilon_0\,,\ j(0) = j_0 \text{ with } j_0 > \varepsilon_0 \tag{3}$$

for the system (2). In Blair's theory excitation occurs at a moment τ at which ε reaches a certain magnitude h which is also considered as a characteristic of the biological system. Thus, from equation (1), the *response time* τ is determined by the relation

$$\sigma^* e^{-\rho\tau} \int_0^\tau e^{\rho t} I(t)\,dt = 1\,, \quad \text{where} \quad \sigma^* = \sigma/h\,. \tag{4}$$

In Rashevsky's theory the excitation occurs when $\varepsilon = j$, and the relation determining the response time τ can be put in a form similar to equation (4). In fact, putting $\overline{\varepsilon} = \varepsilon - \varepsilon_0$, $\overline{j} = j - j_0$, and omitting the bars for simplicity, equations (2)—(3) become

$$\begin{cases} d\varepsilon/dt = \sigma_\varepsilon I - \rho_\varepsilon \varepsilon, & \varepsilon(0) = 0, \\ dj/dt = \sigma_j I - \rho_j j, & j(0) = 0, \end{cases} \tag{5}$$

and the condition of excitation $\varepsilon = j$ becomes $\varepsilon - j = j_0 - \varepsilon_0 = H$. Thus, through the use of equation (5), the response time τ is determined in Rashevsky's theory by the relation:

$$\begin{aligned} &\sigma_\varepsilon^* \exp(-\rho_\varepsilon \tau) \int_0^\tau \exp(\rho_\varepsilon t) I(t)\, dt \\ &\quad - \sigma_j^* \exp(-\rho_j \tau) \int_0^\tau \exp(\rho_j t) I(t)\, dt = 1, \end{aligned} \tag{6}$$

where $\sigma_\varepsilon^* = \sigma_\varepsilon / H$, $\sigma_j^* = \sigma_j / H$. It is known that equation (6) is also obtainable from Hill's theory. Blair's theory involves two independent parameters (σ^*, ρ) and Rashevsky's theory involves four (σ_ε^*, ρ_ε, σ_j^*, ρ_j). Both theories consist of associating a time τ with each function $I(t)$; equation (4) or (6) determines τ as a *functional* of the stimulus $I(t)$.

The propagation of excitation is examined in this paper on the basis of equation (6) in a similar manner as it has been done on the basis of Blair's theory (Opatowski, 1950). Following Rashevsky's treatment we consider a nerve fiber to which a constant current I_0 is applied at one end, $x = 0$. Assuming the fiber to be of infinite length, the longitudinal current at a distance x from $x = 0$ is, in the steady state,

$$I = I_0 e^{-\beta x}, \tag{7}$$

where β is a constant dependent on geometric and electric characteristics of the fiber. If a possible contribution of internal energy sources to the process of excitation is neglected, the substitution of equation (7) into (6) determines a function $x(\tau)$ which describes the propagation of excitation:

$$\begin{aligned} &(\sigma_\varepsilon^* / \rho_\varepsilon)[1 - \exp(-\rho_\varepsilon \tau)] \\ &\quad - (\sigma_j^* / \rho_j)[1 - \exp(-\rho_j \tau)] = e^{\beta x} / I_0 . \end{aligned} \tag{8}$$

The velocity of propagation of excitation $dx/d\tau$ is obtained by differentiating equation (8):

$$dx/d\tau = I_0 e^{-\beta x} [\sigma_\varepsilon^* \exp(-\rho_\varepsilon \tau) - \sigma_j^* \exp(-\rho_j \tau)] / \beta . \tag{9}$$

If x is eliminated here by means of equation (8) an explicit expression of the time dependence of this velocity is obtained:

$$\beta \frac{dx}{d\tau}$$

$$= \frac{\sigma_\varepsilon^* \exp(-\rho_\varepsilon \tau) - \sigma_j^* \exp(-\rho_j \tau)}{(\sigma_\varepsilon^*/\rho_\varepsilon) - (\sigma_j^*/\rho_j) - (\sigma_\varepsilon^*/\rho_\varepsilon)\exp(-\rho_\varepsilon \tau) + (\sigma_j^*/\rho_j)\exp(-\rho_j \tau)}. \tag{10}$$

A comparison of equations (6) and (4) shows that *if* $\rho_\varepsilon = \rho_j$ *the two-factor theory reduces to the one-factor theory* with $\rho = \rho_\varepsilon = \rho_j$ and $\sigma^* = \sigma_\varepsilon^* - \sigma_j^*$. Therefore *if the two-factor theory is to yield more than a mere correction of the results of the one-factor theory, the constants* ρ_ε *and* ρ_j *must not only be different but also of different orders of magnitude.* As a matter of fact, this is the actual situation in the experiments analyzed by A. V. Hill et al in which ρ_j is, in general, 10 to 200 times smaller than ρ_ε; in one case only (frog sciatic nerve) this ratio reaches a value as low as 1.6.

Since there are experimental indications that the velocity of excitation does not vary greatly during its propagation it is of interest to discuss such *approximate* independence of $dx/d\tau$ from τ, on the basis of equation (10). Since the right-hand side of this equation cannot be made exactly independent of τ for any choice of the constants, the velocity of propagation cannot be exactly constant in a mathematical sense.

The velocity of propagation of excitation at $x = 0$ is obtained from equation (9) by putting $x = 0$ and $\tau = \tau_0$, where τ_0 is the response time at $x = 0$. A necessary condition for the excitation to propagate at all is $dx/d\tau > 0$ at $x = 0$. Therefore, if the right-hand side of equation (10) has a positive zero, $\tau = \bar{\tau}$, the latter must be larger than a possible duration of propagation of excitation along a whole nerve because otherwise $dx/d\tau$ could not be approximately constant. But from the numerator of the right-hand side of equation (10) we have:

$$\bar{\tau} = (\rho_j - \rho_\varepsilon)^{-1} \ln(\sigma_j^*/\sigma_\varepsilon^*).$$

Thus even if $\rho_j << \rho_\varepsilon$, so that $\rho_j - \rho_\varepsilon$ is numerically large, a choice of a sufficiently small σ_j^* with respect to σ_ε^* will make $\bar{\tau}$ as large as desired. That such a choice of constants in principle does not contradict equation (8) can be seen in the following manner. Since, according to our discussion, $\rho_j/\rho_\varepsilon = r$ and $\sigma_j^*/\sigma_s^* = s$ have to be assumed small numbers, we have from equation (8):

$$\rho_\varepsilon e^{\beta x}/(\sigma_\varepsilon^* I_0) = 1 - \exp(-\rho_\varepsilon \tau)$$
$$- (s/r)[1 - \exp(-r \rho_\varepsilon \tau)] \approx 1 - \exp(-\rho_\varepsilon \tau) - s \rho_\varepsilon \tau,$$

which is positive because of the smallness of s, as it should be. Thus *an approximate constancy of the velocity of propagation of excitation seems to be compatible with the two-factor theory even if one neglects any possible contribution of internal energy sources to the process of excitation.* Lack of sufficient information on the magnitude of the constants appearing in the theory makes it impossible to arrive at more definite conclusions.

N. Rashevsky assumed that the mathematical expression of the distribution of the current during excitation was obtained by a rigid displacement of function (7) along the x-axis with $x = 0$ always at that point of the fiber which was excited at the moment considered. This can be looked upon as a way of taking into account the contribution of internal energies to the process of propagation of excitation. It can be easily seen that such a theory cannot lead to a mathematically constant velocity of conduction of excitation, although it is compatible with an approximately constant velocity as has been shown by Rashevsky.

In fact, if $\xi(t)$ is the distance covered by the excitation during time t, equation (7) must be replaced now by:

$$I = I_0\, e^{-\beta x + \beta \xi(t)}. \tag{11}$$

Putting, for $n = \varepsilon, j$:

$$J_n = I_0\, \sigma_n \exp(-\rho_n t - \beta x) \int_0^t \exp[\rho_n T + \beta\, \xi(T)]\, dT$$

we obtain from equation (5):

$$\varepsilon - j = J_\varepsilon - J_j\,. \tag{12}$$

By an argument similar to that used by the author in connection with Blair's theory (Opatowski, 1950), the velocity of propagation of excitation is constant if, and only if, $[\partial(\varepsilon - j)/\partial x]_{\text{exc}}$ and $[\partial(\varepsilon - j)/\partial t]_{\text{exc}}$, calculated from equation (12), are constant, where the subscript exc indicates that the functions in the brackets are to be computed at that time t at which the point x becomes excited, the condition of excitation being $\varepsilon - j = H$. Since $[x]_{\text{exc}} = \xi(t)$ it is seen from equation (12) that

$$[\partial(\varepsilon - j)/\partial x]_{\text{exc}} = -\beta H = \text{constant},$$
$$[\partial(\varepsilon - j)/\partial t]_{\text{exc}} = I_0(\sigma_\varepsilon - \sigma_j) + [\rho_j J_j - \rho_\varepsilon J_\varepsilon]_{\text{exc}}\,.$$

But $[J_\varepsilon - J_j]_{\text{exc}} = [\varepsilon - j]_{\text{exc}} = H$; consequently the right-hand side of the last equation is constant if, and only if, $\rho_j = \rho_\varepsilon$, but this cannot be accepted because it would reduce the two-factor theory to the one-factor theory.

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A NOTE ON FACILITATION AND THRESHOLD PHENOMENA

Norman Anderson and Anatol Rapoport
The University of Chicago and Committee on Mathematical Biology,
The University of Chicago

A neuron subjected to a Poisson shower of stimuli responds only if h stimuli impinge upon it within the time interval σ. It is shown that the derivative of the input-output curve cannot exceed unity.

One of the authors (Rapoport, 1950) derived the input-output curve for a single neuron under the following conditions:

1. The neuron is subject to a Poisson shower of stimuli.
2. The neuron responds only to the hth stimulus of a group which falls within the interval σ, provided none of the h stimuli impinges during the refractory period δ.

The expression for the input-output curve turned out to be

$$f(x, \sigma, \delta, h) = \frac{x[1 - e^{-x\sigma} E_{h-2}(x\sigma)]}{\delta x[1 - e^{-x\sigma} E_{h-2}(x\sigma)] + 1 + (h-1)[1 - e^{-x\sigma} E_{h-1}(x\sigma)]}, \tag{1}$$

where $E_k(z) = \sum_{j=0}^{k} z^j/j!$.

The shape of the curve is sigmoid (cf. Rapoport, 1950, Fig. 3). A question naturally arises whether by a proper choice of the parameters, σ, δ, and h, the curve can be made to exhibit a "quasi-threshold" effect, i.e., a sudden rise from a very small value to practically its asymptotic value. Such a "threshold" effect is certainly present if the stimuli are regularly spaced, as has been shown in the above-mentioned paper. It was conjectured, however, that for the case of a Poisson shower (randomized stimuli) no such threshhold effect could be obtained by any choice of parameters. This is in consequence of the fact that the derivative $\partial f/\partial x$ of the input-output curve (1) is bounded for all values of s, σ, δ, and h. This property will now be proved.

In expression (1) call the threshold h_1 instead of h and let $h = h_1 - 2$. We also introduce the following notations

$$a_h(x\sigma) = 1 - e^{-x\sigma} E_h(x\sigma) = e^{-x\sigma} \sum_{h+1}^{\infty} \frac{(x\sigma)^t}{t!}, \tag{2}$$

$$\begin{aligned} D &= \delta x [1 - e^{-x\sigma} E_{h_1 - 2}(x\sigma)] + 1 + (h_1 - 1)[1 - e^{-x\sigma} E_{h_1 - 1}(x\sigma)] \\ &= \delta x a_h + 1 + (h+1) a_{h+1}. \end{aligned} \tag{3}$$

With this notation,

$$f = \frac{x a_h}{\delta x a_h + 1 + (h+1) a_{h+1}}. \tag{4}$$

Let primed quantities represent derivatives with respect to x. Then

$$\begin{aligned} f' &= \frac{1}{D^2}\left[(a_h + x a_h') D - x a_h D' \right] \\ &= \frac{1}{D^2}\Big[(a_h + x a_h')(\delta x a_h + 1 + (h+1) a_{h+1}) - x a_h (\delta a_h + \delta x a_h' \\ &\qquad + (h+1) a'_{h+1}) \Big] \\ &= \frac{1}{D^2}\Big[\delta x a_h^2 + a_h + (h+1) a_h a_{h+1} + \delta x^2 a_h a_h' + x a_h' \\ &\qquad + (h+1) x a_h' a_{h+1} - \delta x a_h^2 - (h+1) x a_h a'_{h+1} - \delta x^2 a_h a_h' \Big]. \end{aligned} \tag{5}$$

Now

$$a_k = -\sigma e^{-x\sigma} \sum_{k+1}^{\infty} \frac{(x\sigma)^t}{t!.} + \sigma e^{-x\sigma} \sum_{k}^{\infty} \frac{(x\sigma)^t}{t!} = \sigma e^{-x\sigma} \frac{(x\sigma)^k}{k!}, \tag{6}$$

and

$$x a_k' = (k+1) e^{-x\sigma} \frac{(x\sigma)^{k+1}}{(k+1)!} = (k+1)(a_{k+1} - a_{k+2}). \tag{7}$$

Thus we see that

$$f' = \frac{1}{D^2}\left[a_h(1 + (h+1)a_{h+1}) - (h+1)(h+2)a_h(a_{h+2} - a_{h+3}) \right.$$
$$\left. + (h+1)(a_{h+1} - a_{h+2})(1 + (h+1)a_{h+1}) \right]. \tag{8}$$

We have $0 < a_{k+1} < a_k \leq 1$ for all k. Also

$$0 < D = \delta x\, a_h + 1 + (h+1)a_{h+1} \geq 1 + (h+1)a_{h+1}. \tag{9}$$

Hence,

$$\begin{aligned} f' &\leq \frac{1}{D^2}\left\{\left[1 + (h+1)a_{h+1}\right]\left[a_h + (h+1)(a_{h+1} - a_{h+2})\right]\right\} \\ &\leq \frac{[1 + (h+1)a_{h+1}][a_h + (h+1)(a_{h+1} - a_{h+2})]}{[1 + (h+1)a_{h+1}]^2} \\ &= \frac{a_h + (h+1)(a_{h+1} - a_{h+2})}{1 + (h+1)a_{h+1}}. \end{aligned} \tag{10}$$

Then $f' \leq 1$, since

$$\frac{a_h + (h+1)(a_{h+1} - a_{h+2})}{1 + (h+1)a_{h+1}} \leq 1. \tag{11}$$

This last inequality is true because $a_h \leq 1$ and $(h+1)(a_{h+1} - a_{h+2}) \leq (h+1)a_{h+1}$.

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SUGGESTIONS FOR A MATHEMATICAL BIOLOGY OF SOME CULTURAL DEVELOPMENTS

N. RASHEVSKY
COMMITTEE ON MATHEMATICAL BIOLOGY
THE UNIVERSITY OF CHICAGO

In connection with the author's previous studies on the effects of imitation in social behavior it is shown how, owing to such effects, two societies which are both characterized by the same distribution functions for different abilities and tastes may differ very greatly in their respective outputs of scientific and inventive work. The course of development which occurs in a given society may be determined by purely accidental initial conditions. A theory of quantitative relations between some cultural and socioeconomic quantities is suggested.

It is now generally accepted that human races do not differ appreciably from each other with respect to their mental abilities. Inasmuch as within any given race different mental abilities vary from individual to individual and are distributed within the population according to some distribution function a precise comparison of different races requires a comparison of those distribution curves. While such comparisons are, perhaps, not available with sufficient precision, it is plausible to assume that those distribution curves are the same for different races. But if so, the incidence of genius in a given field should be the same for all races. The circumstance that this is patently not the case must then be explained as being due to cultural, learned conditions, as well as to differences in environment. This is plausible enough, and may be considered as a good qualitative theory. As always, however, a real check by observation is possible only with a quantitative theory. In this paper we shall outline a quantitative approach to the problem. If developed, this approach should enable us not only to understand the reasons for differences in certain types of achievement in different races, but should also lead to quantitative relations which are verifiable by observation.

In chapter xii of our book (Rashevsky, 1950) we have considered the effects of imitation upon the behavior of a social group in which each individual can exhibit one of two mutually exclusive behaviors, R_1 or R_2. The tendency of each individual toward either R_1 or R_2 is measured by a neurobiophysical quantity ϕ. Positive values of ϕ mean a preference for R_1. Negative values mean a preference for R_2. The larger the absolute value of ϕ, the greater the corresponding preference. An individual with $\phi = 0$ has no preference for either R_1 or R_2.

We have seen that, even if the distribution function $N(\phi)$ of the quantity ϕ in the population is symmetric with respect to $\phi = 0$ so that on the average there is no preference for either R_1 or R_2 in the population as a whole, nevertheless, owing to imitation, the majority of the population will exhibit either R_1 or R_2, depending upon purely accidental initial conditions.

The behaviors R_1 and R_2 may be of any kind. Thus R_1 may stand for a particular fashion in dress, R_2 for a different fashion. Or R_1 may stand for militaristic, R_2 for pacifistic behavior. We may, therefore, also consider R_1 as representing a behavior which consists of the avoidance of any except the most necessary activity. The Italians call it *dolce far niente.* In common English parlance it is known as laziness. The opposite behavior to that, namely R_2, is an activity sometimes beyond the bounds required for the satisfaction of our daily needs. Such men as scientists, inventors, and artists exhibit for the most part behavior R_2. It is legitimate to apply the conclusions of *loc. cit.* to the case of those two mutually exclusive behaviors. There hardly can be any doubt that the attitude of an individual toward work is determined not only by his innate laziness or industriousness, in other words his ϕ, but also by the behavior of the other members of the society in which he lives (the quantity ψ of *loc. cit.*).

Now let us consider the following theoretical case. Let us take two societies, I and II, which have the same distribution function $N(\phi)$. Let us further consider, for simplicity, the case in which $N(\phi)$ is symmetric with respect to $\phi = 0$. However, let society I be in a configuration in which R_1 is preponderant, while in society II R_2 is preponderant. We shall speak of configurations R_1 and R_2 correspondingly. As in *loc. cit.* we shall denote by X_1 the number of individuals which exhibits R_1 in society I, in the stable configuration, while Y_1 shall denote the number of individuals which exhibits R_2 in society I. For society II we shall denote the corresponding quantities by X_2 and Y_2. Let N_1 and N_2 be the number of individuals in the two societies. Because of the symmetry of $N(\phi)$, it follows from *loc. cit.* that

$$\frac{X_1}{N_1} = \frac{Y_2}{N_2} = \alpha; \qquad (1)$$

$$\frac{Y_1}{N_1}=\frac{X_2}{N_2}=1-\alpha. \tag{2}$$

The X_1 individuals in society I will do only the minimum amount necessary to keep them alive, while the Y_1 individuals will apply themselves to all kinds of different activities above and beyond their minimum needs. Under rather general conditions, as we saw in *loc. cit.*,

$$1-\alpha<<1. \tag{3}$$

Thus society I will consist mainly of poor individuals without any interests outside of their minimum daily requirements. On the other hand, society II will produce considerably more than its necessary average minimum subsistence.

As was said above, men like scientists and inventors exhibit behavior R_2, and hence have a large negative ϕ. But a large negative ϕ is certainly not enough to make an individual an inventor or scientist. He also needs sufficiently high ability. While scientific and inventive ability are probably of a rather complex nature and involve a large number of factors, we shall, for simplicity, consider here the theoretical case of only one ability a, distributed according to a distribution function $V(a)$, such that

$$\int_0^\infty V(a)\,da=1. \tag{4}$$

Let both societies have the same $V(a)$.

But a large a does not insure that a man will become a scientist, inventor, or artist. He must have both a large a and a large negative $\phi+\psi$, that is, he must have a large a and at the same time exhibit behavior R_2. There are individuals with undoubted talent who never achieve anything because of behavior R_1. The classical Russian literature is full of such types, the most typical being Goncharoff's Oblomoff.

If we arbitrarily consider an individual as outstanding or a genius if his a exceeds a prescribed value a^*, then, putting

$$\int_{a^*}^\infty V(a)\,da=\beta, \tag{5}$$

we find from (2) and (5) that the percentage G_1 of scientists and inventors in society I is equal to

$$G_1=(1-\alpha)\beta, \tag{6}$$

while the percentage G_2 of scientists and inventors in society II is given by

$$G_2 = \alpha \beta \, . \tag{7}$$

In the case in which inequality (3) holds, we have

$$G_1 << G_2 \, . \tag{8}$$

The value of $1 - \alpha$ may be as small as .01 or even less. In that case

$$\frac{G_2}{G_1} \geqslant 10^2 \, .$$

The actual situation is much more complex. We shall now consider a slightly more complex and realistic case.

As we have seen, society II produces more goods and commodities of all kinds than society I. In monetary terms we may say that its average per capita income i is larger. The income of society I will be distributed according to some distribution function $U_1(i)$, such that

$$\int_0^\infty U_1(i) \, di = 1 \, . \tag{9}$$

The income of society II will be distributed according to a corresponding function $U_2(i)$. Several possibilities may be considered. All individuals who exhibit R_2 may belong to the higher income bracket. This is a rather natural assumption. Or this may not be strictly the case, but negative values of $\phi + \psi$ and income may be positively correlated. Finally, we may consider the case in which there is no correlation between ϕ and i. We shall consider here only the last case, without prejudice to the other two. The case is not so unnatural as it may first seem. While, say, in society I Y_1 individuals exhibit R_2 at any given time, the group Y_1 is not composed of the same individuals at different times. Moreover, as we saw in chapter ix of *loc. cit.*, pure chance may perhaps play a role in the distribution of wealth.

Scientific, artistic, and inventive activities are, as a rule, not remunerative per se. While in some contemporary societies some inventors have become wealthy through their inventions, the opposite seems to have been the rule in the course of even recent history. Maxwell probably never dreamed of the wealth which his discoveries would bring half a century later to General Electric, Westinghouse, and the Edison Companies.

A non-remunerative occupation can be pursued essentially only in hours of leisure, when one is free from the toil for survival. Within limits we consider that the greater the income of an individual, the more leisure time he has. Perhaps it is better to consider in this connection accumulated wealth w rather than income. A businessman who has a large income primarily because he bends all his efforts to making money may have no leisure time at all. A man who inherits wealth may have plenty of leisure time. An individual who has to work 12 hours a day to make a bare living does not have time to meditate on the Theory of Relativity. Thus, in general, the greater w, the greater the available fraction θ of time which an individual may devote to science, art, or invention. Inasmuch as $\theta < 1$, the θ, w curve must approach 1 asymptotically as w increases.

The results of any scientific or inventive activity depend on the one hand on the ability of the individual, on the other on the amount of time he puts into this activity. The greater θ, the less may be a, in order to achieve definite valuable results. Since we consider here the case in which θ is a monotonic increasing function of w, we may say that in a group of individuals with a given w only those will contribute to science and invention for whom

$$a \geqslant u(w), \tag{10}$$

where $u(w)$ is a monotone decreasing function of w. It may, for example, be of the form

$$u(w) = \frac{1}{w} + a^*; \tag{11}$$

where a^* has the same meaning as in equation (5). Expression (11), together with (10), implies that even for a very high w, when θ is practically equal to 1, a minimum ability a^* is necessary to make a good scientist or inventor.

Consider now society I. With the assumptions made above the distribution of wealth among the Y_1 individuals is given by the same distribution function as the distribution of wealth in the whole society. Actually the distribution curves of income and wealth are very similar and we may, therefore, assume that w is distributed in the same way as is i. In a group with a given w the fraction of scientists or inventors is given by

$$\int_{u(w)}^{\infty} V(a)\,da = T(w). \tag{12}$$

Hence the fraction of individuals who have wealth between w and $w + dw$ and who are scientists or inventors is equal to

$$(1-a)\,T(w)\,U_1(w)\,dw\,, \tag{13}$$

and the total fraction in the whole population at all levels of wealth is

$$G_1 = (1-a) \int_0^\infty T(w)\,U_1(w)\,dw\,. \tag{14}$$

Similarly, for society II we find

$$G_2 = a \int_0^\infty T(w)\,U_2(w)\,dw\,. \tag{15}$$

Denoting by $\overline{T}_1$ and $\overline{T}_2$ the mean values of $T(w)$ in the two societies, we may write equations (14) and (15) thus

$$G_1 = (1-a)\,\overline{T}_1\,; \tag{16}$$

$$G_2 = a\,\overline{T}_2\,. \tag{17}$$

If, as would naturally be the case, $V(a)$ is zero for $a = 0$, has a maximum for a positive value a_m of a, and tends to zero for $a = \infty$, then the function

$$f(u) = \int_u^\infty V(a)\,da \tag{18}$$

has the value one for $u = 0$ and decreases to zero as u tends to infinity, having an inflection point for $u = a_m$. If $u(w)$ is of the form (11) or of a similar form, then $T(w)$ is zero for $w = 0$ and tends to 1, which value it reaches asymptotically. If, as a very crude approximation, we put, with γ as a constant,

$$T(w) = \gamma\, w \tag{19}$$

with the range $0 < w < 1/\gamma$, then $\overline{T}_1$ and $\overline{T}_2$ become proportional to the corresponding average per capita wealth w_1 and w_2 in the two societies. Then we find

$$G_1 = (1-a)\,\gamma\,\overline{w}_1\,, \tag{20}$$

$$G_2 = a\,\gamma\,\overline{w}_2\,, \tag{21}$$

and

$$\frac{G_2}{G_1}=\frac{a}{1-a}\frac{\overline{w}_2}{\overline{w}_1}. \tag{22}$$

Since, as we have said, $\overline{w}_2 > \overline{w}_1$, the ratio G_2/G_1 is now even greater than the one calculated from equations (6) and (7). If we assume that the average per capita wealth is proportional to Y/X, which is certainly not true, we find, approximately,

$$\frac{\overline{w}_2}{\overline{w}_1}=\frac{a}{1-a}, \tag{23}$$

and

$$\frac{G_1}{G_2}=\frac{a^2}{(1-a)^2}. \tag{24}$$

With this assumption G_1/G_2 could easily be of the order of 10^4. Actual ratios observed between per capita incomes in western industrialized countries and the "underdeveloped" countries are of the order of 10 or higher. Thus even if G_2/G_1 is not as large as 10^4, it may well be of the order of 10^3.

The situation may be complicated further by studying the following two effects:

a) The effect of a large G on $\overline{w}$. The quantity $\overline{w}$ is itself an increasing function of G.

b) The effect of what may be called the imitation of past generations. The scientific output of the past generation may serve as a stimulus toward scientific activity in the present generation.

Thus we see that two societies, having the same distribution of psychological traits and abilities, may differ tremendously in their scientific and engineering progress.

There are, of course, a number of other factors involved. For example, we may consider the effect of the total population N. Consider two societies both in configuration R_2 and having the same G. If the population N of one society is sufficiently large, so that $GN >> 1$, it will have at any time a sufficient number of scientists and inventors. But if the population N' of the other society is so small that $GN' << 1$, then there will be only one scientist or inventor produced in so many years. If the average time τ between the appearance of such an isolated genius is much longer than the average life span, then there may be difficulty in transmitting results from one scientist to the succeeding one, even though written records may exist. A direct effect of a personal teacher-pupil contact does not exist.

Now let us return to our original two societies I and II. The quantities Y_1 and Y_2 are determined by the intersection of the $F(\psi)$ curve (*loc. cit.*) with the straight line

$$\frac{k}{NA}\psi. \tag{25}$$

The constant k is a purely physiological constant and will, therefore, be assumed independent of N. But A is partly determined by the neurobiophysical parameters, partly by the effectiveness of communication between the individuals in a society (Rashevsky, 1950a). To imitate someone we must have information as to how that individual behaves. Direct information through personal contact, in general, increases with increasing density of population. If S denotes the area occupied by the society, then A may be put proportional to N/S. Denoting by c a constant of proportionality we see that the slope of the straight line (25) is equal to

$$\frac{kS}{cN^2}. \tag{26}$$

The smaller the slope, the more stable the configuration of either R_1 or R_2. But the smaller the slope, the less $1 - \alpha$. Hence, for the same area, the larger population favors "backwardness" in an "underdeveloped" society and technical progress in a "developed" one. The effect of the area, for the same population, is an opposite one.

Through a process of learning such as that discussed in chapter xxii of *loc. cit.*, a transition from behavior R_1 to R_2 may result. It is somewhat more difficult to conceive of a transition in the opposite direction with a mechanism such as described in chapter xxii of *loc. cit.* Such a transition would result in the stagnation of a hitherto developing high technological civilization. Perhaps calamities, affecting all levels of the society and resulting in a kind of general frustration, might produce such a result.

In conclusion it should be emphasized that similar effects may be obtained if R_1 and R_2 denote some types of behaviors other than those discussed above. For example, R_1 may designate a behavior which emphasizes acceptance on faith and development of strong dogmatic religious beliefs, while R_2 consists of a logical analysis of everything. The quantity ϕ in that case may stand for $\varepsilon_c - \varepsilon_r$ of the preceding paper (Rashevsky, 1951).

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OUTLINE OF A MATHEMATICAL BIOSOCIOLOGY OF BELIEFS AND PREJUDICES

N. RASHEVSKY
COMMITTEE ON MATHEMATICAL BIOLOGY
THE UNIVERSITY OF CHICAGO

Behavior based on acceptance on faith is considered as a result of a special conditioning, and is assumed to be mediated through a special center. Behavior based on rational critical analysis is mediated through a different center. The previously developed theory of two mutually exclusive behaviors is applied to the situation. Making simple assumptions about the development of the two centers with age, it is shown how equations can be derived which describe the percentage of individuals exhibiting one type of behavior or another as a function of time and of different biosociological parameters.

In chapter xxi of our book (Rashevsky, 1950) a neural mechanism was suggested which might possibly account for the interplay of the following two opposite types of behavior. One type is the tendency to accept everything uncritically on faith, the other is the tendency to analyze everything rationally. In the neural mechanism outlined therein each of the two behaviors is mediated through a corresponding neural center. Each center is characterized by a level of spontaneous excitation; ε_f for the center which mediates the first type of behavior, ε_r for the center which mediates the second type. The difference

$$\phi = \varepsilon_f - \varepsilon_r \tag{1}$$

determines the relative frequency of one behavior or the other according to equations developed previously (Rashevsky, 1950).

Acceptance on faith may in a sense be considered as a conditioning process. We become conditioned to certain reactions in given situations, and we react in this particular fashion without asking ourselves whether the reaction is logically justified. Beliefs and prejudices, including various religious views, are frequently of the nature of such conditioned reflexes.

If an individual is strongly conditioned at an early age to a specific religious belief, then, even if he later develops his critical reasoning abilities to a high degree, he may have difficulty in abandoning his early established religious beliefs. Devout Catholics among scientists are not rare. Similarly, a man trained in critical reasoning in his own field of investigation may possess racial prejudices which were acquired at an early age.

A certain type of belief or prejudice may be more strongly conditioned than another. The effect of the center for rational reasoning may be opposed not to a general tendency to accept everything on faith, but to a particular situation, accepted on faith by conditioning. Thus for each situation we have an ε_f, which measures the tendency to accept this situation arationally.

It is rather plausible to assume that at birth the individual's center for analytical reasoning practically does not function, so that at birth $\varepsilon_r = 0$. The center for conditioning and for learning certain things mechanically and arationally (Rashevsky, 1950) does, however, function at a very early age, for the child begins to learn some simple reactions very early. We shall, therefore, consider that at birth an individual is endowed with a value or ability to learn which may be measured by a quantity ε_0, and that this value ε_0 is distributed according to some distribution function $V_1(\varepsilon_0)$. If N is the total number of newborn individuals, then

$$NV_1(\varepsilon_0)\,d\,\varepsilon_0 \tag{2}$$

represents the number of newborn individuals who have an ε_0 between ε_0 and $\varepsilon_0 + d\,\varepsilon_0$.

The quantity ε_r increases with age, and, for simplicity, we shall consider a linear increase. If λ and τ^* denote two individual parameters and τ the age, then we have

$$\varepsilon_r = \lambda(\tau - \tau^*). \tag{3}$$

The quantity λ is, in general, different from individual to individual, and is distributed according to some distribution function $V_2(\lambda)$.

The same holds about τ^*, and we should introduce a distribution function for that quantity too. For simplicity, we shall consider here τ^* to be the same for all individuals, thus assuming that the individual variations in the rate of mental development are due to variations of λ only. The reader will easily generalize the subsequent equations to include the variability of τ^*.

As regards ε_f, it may be reasonably assumed to increase with age in proportion to the innate ε_0. If we denote by a a coefficient and by τ_0 the age at which the conditioning of a certain faith reaction begins, then for that particular reaction we have

$$\varepsilon_f = a\,\varepsilon_0(\tau - \tau_0). \tag{4}$$

It must be emphasized that while τ^* is essentially a biophysical constant, τ_0 is a purely sociological one.

At a given moment t let the distribution of the quantity ϕ in the population be given by a function $V(\phi, t)$. From (1), (3), and (4) we have

$$\phi = a\,\varepsilon_0(\tau - \tau_0) - \lambda(\tau - \tau^*). \tag{5}$$

Let N be the total number of newborn individuals at the time $t = 0$. Of those N individuals the number

$$N V_1(\varepsilon_0)\, V_2(\lambda)\, d\,\varepsilon_0\, d\,\lambda \tag{6}$$

will have values of ε_0 and λ in the intervals ε_0, $\varepsilon_0 + d\varepsilon_0$ and λ, $\lambda + d\,\lambda$. At a moment $t > \tau_0$ and $t > \tau^*$ all those individuals will have a ϕ given by expression (5) in which we put $\tau = t$. The number of individuals whose ϕ at the time t is between ϕ and $\phi + d\,\phi$ is equal to the number of individuals whose λ lies between

$$\lambda = \frac{a\,\varepsilon_0(t - \tau_0) - \phi}{t - \tau^*} \tag{7}$$

and

$$\lambda - d\lambda,$$

where

$$d\,\lambda = \frac{d\,\phi}{t - \tau^*}. \tag{8}$$

Introducing (7) and (8) into (6) we find that the number of individuals with a given ε_0 and a ϕ between ϕ and $\phi + d\,\phi$ is given by

$$N V_1(\varepsilon_0)\, V_2\left(\frac{a\,\varepsilon_0(t - \tau_0) - \phi}{t - \tau^*}\right) \frac{1}{t - \tau^*}\, d\,\varepsilon_0\, d\,\phi. \tag{9}$$

The total number of individuals at the time t having any value of ε_0 and a ϕ in the interval $(\phi, \phi + d\,\phi)$ is given by

$$\frac{N}{t - \tau^*}\, d\,\phi \int_0^\infty V_1(\varepsilon_0)\, V_2\left(\frac{a\,\varepsilon_0(t - \tau_0) - \phi}{t - \tau^*}\right) d\,\varepsilon_0. \tag{10}$$

Let $N(\tau)\,d\,\tau$ individuals be born in the interval of time τ, $\tau + d\,\tau$. At the time t their ages will be $t - \tau$. Hence we see from (10) that at the moment t the number of those individuals with a given ϕ is equal to

$$\frac{N(\tau)}{t-\tau-\tau^*}\,d\phi\,d\tau\int_0^\infty V_1(\varepsilon_0)\,V_2\left(\frac{a\,\varepsilon_0(t-\tau-\tau_0)-\phi}{t-\tau-\tau^*}\right)d\,\varepsilon_0. \tag{11}$$

If we integrate expression (11) with respect to τ between the limits $-\infty$ and t we find the total number of individuals born before the moment t and who at the time t have a ϕ between ϕ and $\phi + d\phi$. Hence that number is given by

$$V(\phi, t)\,d\phi$$

$$= d\phi\int_0^\infty\int_{-\infty}^t \frac{N(\tau)}{t-\tau-\tau^*}\,V_1(\varepsilon_0)\,V_2\left(\frac{a\,\varepsilon_0(t-\tau-\tau_0)-\phi}{t-\tau-\tau^*}\right)d\,\varepsilon_0\,d\,\tau. \tag{12}$$

In deriving expression (12) we neglected those individuals who were born between $t-\tau_0$ and t and who have not yet begun to be conditioned. If, as is most likely the case, $\tau^* < \tau_0$, then, at the moment t, for all individuals born in the interval $(t-\tau_0,\, t-\tau^*)$ the quantity ε_r increases, but ε_f remains zero. For individuals born in the interval $(t-\tau^*,\, t)$ both ε_r and ε_f are zero. For all the individuals of the first kind ε_f is zero and ϕ is given by

$$\phi = -\lambda(t-\tau-\tau^*), \quad \tau^* < \tau < \tau_0. \tag{13}$$

The number of individuals born between $t-\tau_0$ and t and having at the time t a given ϕ is, therefore, equal to

$$d\phi\int_{t-\tau_0}^{t-\tau^*}\frac{N(\tau)}{t-\tau-\tau^*}\,V_2\left(\frac{-\phi}{t-\tau-\tau^*}\right)d\,\tau. \tag{14}$$

The total number of individuals who at the time t have a given ϕ, in other words, the expression $V(\phi, t)\,d\phi$, is given by the sum of expressions (12) and (14). Hence

$$V(\phi, t)$$

$$= \int_0^\infty \int_{-\infty}^t \frac{N(\tau)}{t - \tau - \tau^*} V_1(\varepsilon_0) V_2\left(\frac{a\,\varepsilon_0 (t - \tau - \tau_0) - \phi}{t - \tau - \tau^*}\right) d\,\varepsilon_0\, d\,\tau$$

$$+ \int_{t-\tau_0}^{t-\tau^*} \frac{N(\tau)}{t - \tau - \tau^*} V_2\left(-\frac{\phi}{t - \tau - \tau^*}\right) d\,\tau. \tag{15}$$

The function $V(\phi, t)$ thus contains as a parameter the quantity τ_0, which is the age at which the conditioning to a certain belief or prejudice begins.

We may generalize expressions (12) and (15) by considering that the coefficient a varies from individual to individual and that its distribution is the same as the distribution of ϕ at the moment $\tau + \tau_0$ when the conditioning process begins. This is rather plausible because the larger the number of individuals with a positive ϕ, the stronger will be the effort to condition other individuals toward a faith behavior. This stronger effort may be expressed as a larger value of a. Instead of (15) we now have:

$$V(\phi, t) = \int_0^\infty \int_{-\infty}^t \int_0^\infty \frac{N(\tau)}{t - \tau - \tau^*} V_1(\varepsilon_0) V_2\left(\frac{a\,\varepsilon_0 (t - \tau - \tau_0) - \phi}{t - \tau - \tau^*}\right)$$

$$\cdot V(a, \tau + \tau_0)\, d\,\varepsilon_0\, d\,\tau\, da + \int_{t-\tau_0}^{t-\tau^*} \frac{N(\tau)}{t - \tau - \tau^*} V_2\left(-\frac{\phi}{t - \tau - \tau^*}\right) d\,\tau, \tag{16}$$

which is a peculiar type of functional equation for the determination of $V(\phi, t)$.

Once the function $V(\phi, t)$ is known we also know the percentage of individuals who behave rationalistically and do not accept anything on faith. In particular, if the beliefs in question are religious beliefs, then the above percentage is also the percentage of agnostics in the population.

Let $P_a(\phi)$ be the percentage of agnostics among all individuals with a given ϕ. The function $P_a(\phi)$ is determined by equations (21) and (22) of chapter ii of our book (Rashevsky, 1950). The fraction of agnostics $p(t)$ in the whole population at a given time t is

$$p(t) = \int_{-\infty}^{+\infty} V(\phi, t) P_a(\phi) \, d\phi \, . \tag{17}$$

Expression (15) or (16), together with (17), gives us the incidence of agnostics at different times in terms of such data as the distribution of learning ability at birth, the distribution of the constant λ, which determines the rate of mental development of an individual, the birth rates at different times in the past, and, finally, the age τ_0 at which religious conditioning begins. In principle all the above functions are determinable experimentally, and thus the equations are verifiable.

It is readily seen that the greater τ_0, that is, the later the conditioning begins, the more rapid will be the shift toward a rational behavior in the social group. Religious beliefs, which are usually acquired at a very early age, are most persistent. Certain political beliefs and prejudices, being acquired at a much later age, are less stably entrenched in the behavior pattern of society.

If, as a rough approximation, we consider that an individual practically always behaves as an agnostic when his ϕ is below a fixed negative value ϕ_0, then, denoting by $U(a)$ the distribution function of a at the time of birth, we find from expression (10) that the number $N_a(\tau)$ of individuals who become agnostic at the age τ is given by

$$\begin{aligned} N_a(\tau) = \frac{N}{\tau - \tau^*} \int_{-\infty}^{\phi_0} d\phi \int_0^{\infty} \int_0^{\infty} V_1(\varepsilon_0) \\ \times V_2\left(\frac{a \, \varepsilon_0 (\tau - \tau_0) - \phi}{\tau - \tau^*} \right) U(a) \, d\varepsilon_0 \, da. \end{aligned} \tag{18}$$

By introducing effects of imitation, as was done in chapter xiii of *loc. cit.*, we may study such cases as transition from agnosticism to religiousness of individuals who were born and initially raised in agnostic surroundings, and for whom initially $a = 0$.

The solution of the functional equation (16) is probably difficult, but if we use the simpler expression (15), then $V(\phi, t)$ may be evaluated by quadratures. We may assume various plausible distribution functions for $N(\tau)$, $V_1(\varepsilon_0)$, and $V_2(\lambda)$.

Instead of equation (3) we may consider the case in which ε_r begins to increase at the age τ^* according to

$$\frac{d\,\varepsilon_r}{dt}=\lambda-\kappa\,\varepsilon_c\,, \tag{19}$$

where κ is a constant. Integrated this gives

$$\varepsilon_r=\frac{\lambda}{\kappa}\left(1-e^{-\kappa(t-\tau^*)}\right). \tag{20}$$

In this case if $\tau_0 < \tau^*$ and $\lambda > a\,\varepsilon_c$, the quantity ϕ may first be positive, then become negative, and then again become positive. Such an individual becomes agnostic at a certain age, but later on, at a more advanced age, again becomes religious. The smaller κ, the more advanced the age at which ϕ again becomes positive; in other words, at which the early conditioned beliefs again return.

As a crude approximation, the following simple treatment of some of the above problems may be suggested. Let the total population n increase according to

$$\frac{dn}{dt}=\beta\,n\,, \tag{21}$$

where β is a constant. Thus, if n_0 is the value of n at $t=0$,

$$n=n_0\,e^{\beta t}. \tag{22}$$

Let a fraction α of the newborn individuals eventually become agnostic through a mechanism discussed above. And let us furthermore assume that individuals born of agnostic parents and raised as agnostics permanently remain such. If n_1 is the number of agnostics, then

$$\frac{dn_1}{dt}=\beta\,n_1+\alpha\,\beta(n-n_1)\,. \tag{23}$$

Equations (22) and (23) give:

$$\frac{dn_1}{dt}=\alpha\,\beta\,n_0\,e^{\beta t}+\beta(1-\alpha)\,n_1. \tag{24}$$

Integrated with the initial condition $n_1=0$ for $t=0$, equation (24) gives

$$\frac{n_1}{n}=1-e^{-\alpha\beta t}. \tag{25}$$

With $\beta\sim10^{-2}$ year^{-1} and $\alpha\sim10^{-2}$, we find $\alpha\,\beta\sim10^{-4}$. Hence a completely agnostic behavior will be approached by society in about 10^4 years. If $a \sim 10^{-4}$, the necessary time becomes $\sim 10^{-6}$ years.

If a fraction γ of those born in agnostic families eventually become religious as a result of imitation, then we obtain a nonlinear equation

$$\frac{dn_1}{dt} = \beta n_1 + \alpha \beta (n - n_1) - \kappa (n - n_1) n_1. \tag{26}$$

A further elaboration of this approach will also have to take into consideration the mortality rate.

LITERATURE

Rashevsky, N. 1950. *Mathematical Biology of Social Behavior.* Chicago: University of Chicago Press.